MONOGENETIC TREMATODES

THEIR SYSTEMATICS AND PHYLOGENY

by

B. E. Bychowsky

English Editor

WILLIAM J. HARGIS, JR.

TRANSLATION OF A RUSSIAN MONOGRAPH | NINTH IN A SERIES

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Monogenetic Trematodes

Their Systematics and Phylogeny

АКАДЕМИЯ НАУК СССР
ЗООЛОГИЧЕСКИЙ ИНСТИТУТ

Б. Е. БЫХОВСКИЙ

МОНОГЕНЕТИЧЕСКИЕ СОСАЛЬЩИКИ

ИХ СИСТЕМА И ФИЛОГЕНИЯ

ИЗДАТЕЛЬСТВО
АКАДЕМИИ НАУК СССР
МОСКВА-ЛЕНИНГРАД
1957

Monogenetic Trematodes

Their Systematics and Phylogeny

by

BORIS E. BYCHOWSKY

Edited
by
WILLIAM J. HARGIS, JR.

Translated
by
PIERRE C. OUSTINOFF

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LIBRARY

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Preface
to Translation[1]

Translation of this monograph, undoubtedly the most valuable one written to date on this group of parasites, was undertaken as part of a long-term research project on the systematics, host-specificity and zoogeography of monogenetic trematodes.[2] Translation and editing were accomplished in the following manner:

1. Having previously checked difficult words, Oustinoff[3] read sight translation to Hargis.
2. Hargis, partially editing, wrote translation in long hand.
3. Hargis and Oustinoff edited this manuscript and Hargis put translation on tape.
4. Miss Conner transcribed translation from tape to first typescript.
5. Hargis edited typescript again.
6. Miss Conner retyped.
7. Hargis and Oustinoff re-edited by comparing typescript with book for content.
8. Typescript retyped by Miss Conner.
9. Dr. and Mrs. Oustinoff re-edited against text.
10. Hargis again edited typescript for final corrections.

This project, begun in September of 1958, has taken over two and one-half years to complete.

A conscious effort has been made to keep this translation as near the original as possible. It is probably inevitable, however, that some of the nuances of meaning in the original have been distorted or lost. For this we apologize to Dr. Bychowsky and the reader.

---

[1] Virginia Institute of Marine Science Translation Series, Number 1.

[2] Translation and editing supported by funds from Grant No. E-2389 of the National Institutes of Health. Publication under auspices of AIBS Translation Series supported by Grant No. G14802 from the National Science Foundation.

[3] Chairman, Department of Modern Languages, College of William and Mary, Williamsburg.

Certain passages were difficult to translate. Most troublesome were: *закономерность*, which literally is "lawful measure" but which may be translated variously as--conformity with law, regularity, principle, normality; and *зеркальный*, which is translated as smooth or bilaterally symmetrical. In the case of the former word, several alternative translations are usually given where it occurs in the text. Where a different English phrase seems to fit Dr. Bychowsky's meaning better or serves to clarify the text, it has been inserted in parentheses with the Latin notation *nobis*--by us. To avoid lengthy rendition of the original, we have at times used new words the meaning of which seems, nevertheless, clear. For instance, we have translated *mnogoletnii* by *polyannual* to designate a cycle which lasts many years, and *segoletki* by *young of the year* to designate fishes which are less than one year old. Certain obvious errors or misspellings in the original text were changed, less obvious ones are noted with (*sic*).

The bibliography was divided into two parts, Russian and non-Russian, in the original and has been retained that way in the translation. The Library of Congress system for the spelling of the names of Russian authors has been followed in the bibliography. When the name of the author was spelled differently in a previous translation, the alternate spelling follows our transliteration. The reason for this is that for purposes of research it is preferable to follow the system of the Library of Congress which indicates variant spellings.

To prevent misunderstanding which may have arisen from the preservation of Russian letters used in the original to identify the drawings, we replaced, in the translation, Russian letters by those of the English alphabet, for instance, Russian B by English C, etc. To clarify further this substitution, we have reproduced on page iv both alphabets. In so doing, we do not think it out of place to include in parentheses after Russian letters the symbols used for their transliteration. The numerals between the alphabets indicate the relative place of each letter in its respective alphabet.

Though the Latin morphological terms are not italicized in the Russian text, we prefer to do so in the translation.

For convenience in referring to the Russian text the original pagination is given in the margin of the translation opposite the place where the new page begins. Occasionally figures or tables are somewhat displaced from their original page location; however, since they, themselves, are numbered sequentially, no confusion should result.

The citation of numbers for measurements and numbered structures are generally given in the translation as they were in Professor Bychowsky's book. This should further facilitate checking with the Russian.

Aside from the fact that the text is occasionally interlarded with references to dialectical materialism which seems to have little place in this or any other scientific paper, Dr. Bychowsky has produced the best, most comprehensive treatise on monogenetic trematodes ever offered to science. Besides being an excellent account of the biology and systematics of these interesting parasites, the sections on host-parasite relationships and the historical aspects of the general phenomenon of parasitology are noteworthy. Bychowsky's determinations of the phylogenetic relationships among and between the parasitic groups of the Phylum Platyhelminthes and the free-living turbellarians are extremely interesting. Thus, though the book is devoted chiefly to the Class Monogenoidea (Beneden) Bychowsky, 1937, it is a significant contribution to all parasitology.

Thanks are due to Miss Patricia R. Conner of the Virginia Institute of Marine Science who transcribed, typed, and assembled the manuscript, and to Mrs. Ellen Oustinoff, who assisted with final editing.

William J. Hargis, Jr.
Laboratory Director and Dean
School of Marine Science of the College
of William and Mary in Virginia

ALPHABETS

Russian					English
А	а(a)		1		A a
Б	б(b)		2		B b
В	в(v)		3		C c
Г	г(g)		4		D d
Д	д(d)		5		E e
Е	е(e)		6		F f
*Ё	ё			7	G g
Ж	ж(zh)	7		8	H h
З	з(z)	8		9	K k
И	и(i)	9		10	L l
Й	й(ĭ)	10		11	M m
К	к(k)	11		12	N n
Л	л(l)	12		13	O o
М	м(m)	13		14	P p
Н	н(n)	14		15	Q q
О	о(o)	15		16	R r
П	п(p)	16		17	S s
Р	р(r)	17		18	T t
С	с(s)	18		19	U u
Т	т(t)	19		20	V v
У	у(u)	20		21	W w
Ф	ф(f)	21		22	X x
Х	х(kh)	22		23	Y y
Ц	ц(ts)	23		24	Z z
Ч	ч(ch)	24			
Ш	ш(sh)	25			
Щ	щ(shch)	26			
**	ъ(")	27			
	ы(y)	28			
	ь(ʼ)	29			
Э	э(ė)	30			
Ю	ю(i͡u)	31			
Я	я(i͡a)	32			

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* As a rule, ё occupies the same place as e in Russian alphabet.

** The hard sign (") is used only in the middle of a word.

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American biologists, seeking to harness pressure for modernization and coordination, created the American Institute of Biological Sciences to administer programs in behalf of all biology.

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  - Subclass Polyonchoinea
    - Order Dactylogyridae
      - Suborder Dactylogyrinea
        - Family Dactylogyridae
        - Family Diplectanidae
        - Family Protogyrodactylidae
        - Family Calceostomatidae
      - Suborder Monopisthocotylinea
        - Family Monocotylidae
        - Family Loimoidae
        - Family Dionchidae
        - Family Capsalidae
        - Family Acanthocotylidae
        - Family Microbothriidae
    - Order Tetraonchidea
        - Family Tetraonchidae
        - Family Amphibdellatidae
        - Family Tetraonchoididae
        - Family Bothitrematidae
    - Order Gyrodactylidea
      - Suborder Gyrodactylinea
        - Family Gyrodactylidae
      - Suborder Polyopisthocotylinea
        - Family Polystomatidae
        - Family Sphyranuridae
  - Subclass Oligonchoinea
    - Order Diclybothriidea
        - Family Diclybothriidae
        - Family Hexabothriidae
    - Order Chimaericolidea
        - Family Chimaericolidae
    - Order Mazocraeidea
      - Suborder Mazocraeinea
        - Family Mazocraeidae
        - Family Hexostomatidae

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Suborder Discocotylinea
    Family Discocotylidae
    Family Anthocotylidae
    Family Plectanocotylidae
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FOREWORD

Within the last 20 to 25 years an increasing number of works have p. 3
been devoted to the monogenetic trematodes. Despite this, our knowledge is still far behind that of other parasitic groups, particularly digenetic trematodes and tapeworms. For this reason I consider it my duty to publish the results of my almost 30 years of research in the field of phylogeny and systematics of the Monogenoidea considering that, despite the numerous and irritating gaps which are clearly apparent to me, my work nevertheless will be fruitful in the development of further research in this very interesting group in the practical as well as the theoretical sense.

I am prompted to this publication by the memories of constant and friendly exhortations of my teacher, Valentine A. Dogiel, whose desire it was to see this work completed. V. A. Dogiel was vitally interested in these questions which inspired me, and much of what is written here is the result of mutual discussion and lively disputation which took place during all the years of our common work, beginning with the expedition to the Aral and Caspian Seas in 1930-32. It is impossible to express with words the feeling of gratitude which I experienced when I remember and evaluate the influence of V. A. Dogiel on my life and scientific work.

The completion of the present research was greatly impeded by the fact that, until recently, I could only work sporadically because of the overload caused by other duties. Consequently, a warmer feeling comes from the remembrance of constant help and friendly attention which was given my by my friends in the Department of Parasitology and the Ichthyology Laboratory of the Zoological Institute of the Academy of Sciences, U.S.S.R. I also received considerable help from collaborators of the Laboratory of Fish Diseases, VNIORKh (All-Union Scientific Research Institute of the Fish Industry of Lakes and Rivers nobis) and the Department of Invertebrate Zoology of Leningrad University.

Academician E. N. Pavloski, showed constant attention to my work, and he often helped to organize many of my field trips.

During the writing of this work I received great support from two
of my friends, A. A. Strelkow and A. S. Monchadsky without whose help my p. 4
work would have remained unfinished for a long time. Their friendly criticism
and advice constantly helped my work. I must also mention the help of A.
A. Strelkow and many of our common field trips to the Pacific Ocean, the
Sea of Japan and the Sea of Okhotsk.

The shaping up of this work, which required great labor, was accomplished with the collaboration of L. F. Nagibina. The majority of the original drawings were made by her. In addition to that, for many years L. F. Nagibina constantly helped me in my experiments and field trips. The final processing of the drawings was made by the brigade of artists of the Zoological Institute, primarily by N. Liahovi and E. D. Samenskia.

I beg all my friends who cooperated in my work to accept my heartfelt gratitude.

All the drawings which illustrate the present work were made from the ventral views of the whole mounts of the worms. The exceptions are described in the legends. Borrowed drawings are acknowledged with references to the author and the year of publication. The references to location of hosts of monogenetic trematodes are made in the legends of the drawings to permit verification of the correctness of classification, and also in this connection because many of these references will widen the scope of the information about the widespread locations of the hosts of the different types of parasites.

The work was completed in December 1955, and all the literature available to me which had been published up to the middle of 1955 was utilized for it. Unfortunately, certain important works were known to me only by abstracts. Likewise, I was unable to include those papers which appeared during the year and a half which passed from the time of completion to the time of publication. In doing so I missed a certain number of references which cited new data concerning the distribution and biology of monogenetic trematodes, and also which described certain new types and species. The inclusion of all of these references in the present work was impossible. Comments on more important publications were added during the course of reading the proofs, but only as special footnotes. Nevertheless, I believe the existing irritating omissions will not seriously influence the basic conclusions.

B. Bychowsky

INTRODUCTION

p. 5 Our first observations on the monogenetic trematodes were begun during student years at the Institute of Natural History in Peterhof, when in 1927 we became acquainted with the morphology and growth of a series of representatives of the species of *Dactylogyrus* Diesing and later the polystomes of the frog.

The striking resemblance of the larvae of these two groups, despite the great dissimilarities of the adults, forced us to consider the question of family relationships within the limits of the group of the monogenetic trematodes even then. Further work on parasitic worms led to the firm conviction of the necessity for special research on the subjects of phylogeny and interrelationships of the parasitic flatworms. At the same time, the first studies of the monogenetic trematodes convinced us of the essential significance of this group to an understanding of the phylogenies of all of the groups of parasitic worms.

Already in 1932, while examining the interrelationships of the various species of *Gyrodactylus* von Nordmann and *Dactylogyrus* Diesing, we came to the conclusion that it is impossible to understand systematic relationships and phylogeny without careful study of the embryological development of monogenetic trematodes, because, in a number of cases the true relationships are masked by the resemblances of the adults which are connected with the analogous conditions for existence.

About 1935-36 we were convinced of the incorrectness of the widespread view concerning the close kinship between monogenetic and digenetic trematodes, and the monolithic relationship of the group of Cestodaria, and in 1937 we published a work containing an effort to build a system of parasitic flatworms on the basis of the scheme of their phylogenetic interrelationships. This work was primarily preliminary in character because of the insufficiency of factual material. Its publication forced us to pay more attention to the questions of the interrelationships within the class Monogenoidea, inasmuch as it seemed to us that the analyses of these interrelationships would give a more solid base to our entire system. Henceforth, we set for ourselves a problem of studying all aspects of the monogenetic trematodes for the purpose of re-establishing the phylogenesis of the given group and a thorough treatment of its systematics.

p. 6 The study of the interrelationships of many contemporary invertebrates, particularly the worms, presents considerable difficulties because of the absence of fossil remains. As a result, the researcher who is interested in phylogeny is faced with the difficult problem of reconstructing historical processes on the basis of materials dealing with the morphology and life history of contemporary animals. The method of mutual verification of data from the studies of different phenomena of the group under study allows us to reconstruct its past and those genetic links which can be utilized for the building of the system on phylogenetic foundations with a high degree of reliability. It is impossible not to note that parasitic animals are more convenient in this connection because their examination provides supplementary, purely parasitic criteria for the reconstruction of the past history of the group.

It seems to us that the importance of the study of phylogenesis of any given group of animals must not be underestimated. Only the concrete knowledge of the phylogenesis of separate groups permits us to represent in an accurate way a general nature of the evolution of the animal world which has great theoretical significance and which also appears as a basis for the exact classification of animals. Along with this, we are firmly convinced that only an adequate, complete knowledge of the phylogenesis of a gr up can serve as the sufficient basis for the solution of natural methods of its full economic utilization. As applied to the parasitic animals, the knowledge of phylogenesis of a group is indispensable for the correct planning of methods of biological struggle with parasitic diseases, and also for a clear understanding of the potential danger of any single group of parasites or of a specific parasite fauna.

Our research on phylogenesis of parasitic flatworms is still far from complete, but it is already possible to expediently sum up the study of phylogenetic relationships of monogenetic trematodes and also to build a system of the group on the basis of these interrelationships. Our present work is dedicated to these two problems.

Data from the literature and new material collected by us, our students, and colleagues forms the foundation of our system. In many instances the published data, to our regret, are entirely unsatisfactory because the authors did not pay proper attention to certain peculiarities of morphology and embryology which, from our point of view, have the greatest significance. This forced us to re-examine or repeat the experiments which was extremely burdensome because of the difficulty of securing original material. For these basic reasons we were forced to consider with extreme care the data pertaining to the discovery of a particular species of monogenetic trematodes on a particular host. One of the reasons is the inexactitude in identifying the host or parasite. The second, much more com- p. 7
plex, precisely the (reporting of a, nobis) finding of a parasite not on the host peculiar to it in normal conditions, but on the strength of local discovery of the host during the examination or during the capture of the fish host (in the instruments of capture of the fish or during the transport) when a mechanical transfer or an independent transfer from one host to another might occur.

The third and most important reason, which in numerous cases demands special analysis, involves the description of a parasite from a host which is not habitual to it as a result of the grouping for varying periods of time of different species of fishes (mainly in fresh water or in marine display aquaria). We will consider the cases which can be explained by the various reasons later on, but here we must note particularly the necessity of very cautious treatment of the data of MacCallum, who worked in the New York Aquarium and who allowed great inaccuracies to creep into his research.

Systematic and morphological collections of monogenetic trematodes and research with live animals provided the material for this work. The collections of monogenetic trematodes were conducted either by us directly at the place of location of the live hosts or under laboratory conditions from ichthyological collections chiefly from the Zoological Institute of the Academy of Sciences, U.S.S.R. All in all, the collections contain very significant material from the most diversified regions of the Soviet Union and foreign countries. One must especially note material from all the South Seas of Russia, from middle Asia (Region Tschu and Tadjikistan and Turkmania and others), from the far East (Amur River System, the Sea of Japan, the Sea of Okhotsk and the Pacific Ocean), from Japan (fresh water and salt water), from the fresh waters of the Maylayan Archipelago, from the United States of America and Canada, and finally from western Europe (Mediterranean Sea, Atlantic Ocean and others). The smallest quantity of material was received from Africa, South America, and Australia.

The study of live material was conducted by us in the Leningrad region (the Bay of Finland, River Neva and "Ropscha" Fish Farms, small lakes, ponds and brooks) in 1927-1929, 1931-1932, and 1945-1952; on White Lake in 1931; in Karelia (a system of lakes near Konchezero near Peltrolavodsk) in 1932; on the Volga (near Kostroma and Saratov in the Delta) in 1926-27, 1931-32, 1947 and 1953-54; in western Siberia (Barabinskaya Steppe, lakes of the group of Chanov) in 1933; on the Black Sea (Karadag and Sebastopol) in 1927, 1935 and 1947; in the Sea of Azov (in the estuaries of Ahtarinsk) in 1933; the Caspian Sea (on the Island of Sara) in 1931-1932 and 1955; in the sea of Aralsk (Aralsk and Muynak and the islands of Uzun-Kair and Kuzdjk-Pes) in 1930; in Tadjikistan (in region of Stalinbad and Vahsha) in 1943-1945; on the Sea of Japan (the Bay of Peter the Great and the western banks of Sakhalin Island) in 1946 and 1949; on the Sea of Okhotsk (Bay of Aniv and the western Shore of Sakhalin) in 1946 and 1949; in the shallow waters of Kurile (in the Island of Shikotan) in 1949; and in the Pacific Ocean in 1955.

For this work we also utilized the researches on live material which were conducted by colleagues of our laboratory: A. V. Gussew on Hanka Lake, 1948-1949 and in the Barents and Norwegian Seas in 1950; by U. A. Strelkow at the Sebastopol Biological Stations in 1949; and L. F. Nagibina in the Leningrad region in 1946-52; and N. A. Izumova on the Ropscha Fish Farm south of Leningrad in 1951 and 1952. p. 8

The researches on Monogenoidea were carried out in many different ways, from the point of view of biology, morphology and embryology. We gave special attention to work on live materials because it was possible to discover a whole series of structures only in this fashion. Thanks only to the study of live materials was it possible to understand the physiological meaning of a series of morphological peculiarities unknown until the present time. We would also like to underline this circumstance on the strength of the fact that at the present time the study of monogenetic trematodes is based almost entirely upon fixed material which is completely wrong and in many cases leads to erroneous results. It is curious that the researches of the middle of the last century widely utilized live materials, and in many cases their works describe the forms and structure of monogenetic trematodes much more precisely than corresponding data of contemporary authors who are armed with complete microscopic technology but who do not employ direct observation of living organisms.

Unfortunately, we could not utilize the data concerning geographical distribution of monogenetic trematodes because there is still very insufficient data at the present time, and this could have led to faulty conclusions. However, in certain isolated cases distribution was taken into consideration.

PART I

MORPHOLOGY AND BIOLOGY OF MONOGENETIC TREMATODES

Page Numbers In Margins Refer To Original Russian Text

PART I

MORPHOLOGY AND BIOLOGY OF MONOGENETIC TREMATODES

CHAPTER I

MORPHOLOGY OF MONOGENETIC TREMATODES

The present chapter contains a description of the morphology of monogenetic trematodes expressed in such a way as to serve as a basis for further considerations of the evolution of the group. In connection with this, not all parts are described with an equal degree of completeness, and on the other hand, the appraisal of such morphological characteristics is made from the point of view of the phylogenetic researcher and not of the (pure) morphologist. p. 11

We shall also indicate that the material described has, itself, an independent significance, because neither in native nor in foreign literature is there anything comparable at the present time.

In Russian literature monogenetic trematodes, which were separated by us into an independent class (Bychowsky, 1937), are considered with digenetic trematodes.[1] Consequently, as a result of the greater attention to digenetic trematodes, the information on the morphology of the monogenetic trematodes is given in such a fragmented fashion that it completely fails to impart an accurate impression concerning the group.

Among foreign works the most solid description of monogenetic trematodes is the essay of M. Braun (Braun, 1889 to 1893) which became extremely antiquated although, in some respects, it preserves its significance even to the present time. The second among the essays is the work of O. Fuhrmann (Fuhrmann, 1928) very succinctly written by a non-specialist, and it also has become antiquated. During recent years there appeared two more essays concerning the group which interests us, one by Ben Dawes (Dawes, 1947) which is devoted to monogenetic and digenetic trematodes, the other by Nora Sproston (Sproston, 1946) which is devoted especially to monogenetic trematodes. Both essays have sections on morphology, but they are extremely short and serve mainly as an introduction to the systematic parts.

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[1] Referring to textbooks and morphological references, because in literature on systematics our system of parasitic flatworms is acquiring a greater number of adherents.

Abbreviated data on morphology of monogenetic trematodes are scattered in a considerable number of specialized works. The most important are the researches by Zeller (Zeller, 1872-1876), Cerfontaine (Cerfontaine, 1814-1900), and Seitaro Goto (Goto, 1891-1917) who produced a series of very substantial works which contain a significant amount of morphological material along with their systematic material.

Recently, Brinkmann (Brinkmann, 1940-1954) published a series of works which have significance for Monogenoidea and which are p. 12 based, not only on external characteristics, but also on detailed morphological analyses of interior structures.

Literature data and especially the results of personal research were utilized for the present essay.

Sizes. In the majority of cases the sizes of the monogenetic trematodes usually vary between the lengths of 0.03 to 20 mm, and only in rare cases do they reach a larger size. Thus Capsala martinieri Bosc (Fig. 1) reaches 30 mm in length and 25 mm in width, Squalonchocotyle somniosi (Causey) has a length of about 25 mm and probably Sq. borealis (Beneden) (Fig. 2) reaches up to 30 mm, etc. One can consider it a general rule that marine forms are larger than fresh-water forms. It is necessary, however, to note that the measurement of size is hampered by the fact that the body of monogenetic trematodes is capable of contracting and stretching excessively. Most of the species can stretch almost twice, and contract as much in relation to the normal condition of their bodies. Thus, Dactylogyrus auriculatus (Nordmann) (Fig. 3) which is about 0.5 mm in the normal state can stretch to 1.2 mm and contract to 0.3 mm.

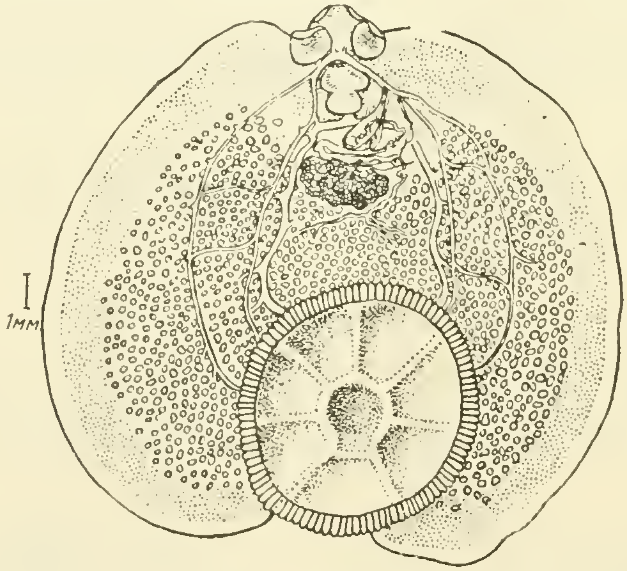

Fig. 1. Capsala martineri Bosc, adult worm. (According to Price, 1939).

Shape of the Body. Bilateral symmetry is the most common, with the longitudinal axis of the body with a narrowed and rounded anterior end, and an adhesive disc on the posterior end which is more-or-less separated from the rest of the body. The ratio between the longitudinal and transverse axis fluctuates significantly in different species. For instance, certain individuals of *Tristoma coccineum* Cuvier (Fig. 4) may be as wide as they are long, and the above mentioned *Squalonchocotyle somniosi* (Causey) has a length which exceeds the width by 11 times. The most common type is 3-4 times longer than wide, as for instance, with the majority of Dactylogyridae (Fig. 5). Along with these bilaterally symmetrical species we also find asymmetrical species such as *Vallisia striata*, Perugia and Parona (Fig. 6), which shows lateral growth in the middle of its body that divides the body into two separate sections. The posterior section is strongly curved and unequally developed in relation to the longitudinal axis. Asymmetry of such a type is undoubtedly a secondary phenomenon. There are also other types of asymmetry, also of secondary origin, but linked to a special type of evolution of the adhesive apparatus. The latter, in a series of cases, develops only from one side of the body, thus resulting in asymmetry, nevertheless the internal structures of the body remain bilaterally symmetrical. In other cases, which are superficially similar but different in nature, asymmetry results from the displacement of the symmetrical adhesive disc toward one side of the body of the animal. Examples of asymmetry of the first type can be seen in representatives of the species of *Gastrocotyle* (Fig. 7) and the second type in the species of *Axine* (Figs. 8 & 9).

p. 13

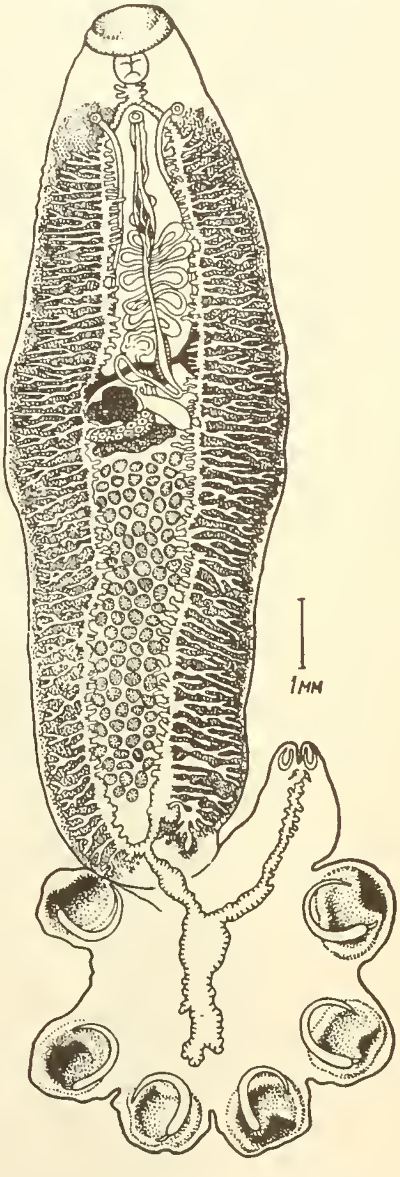

Fig. 2. *Squalonchocotyle borealis* (Beneden), adult worm from the gills of *Somniosus microcephalus* (Bl. and Schn.) near the banks of Murman (Barents Sea)

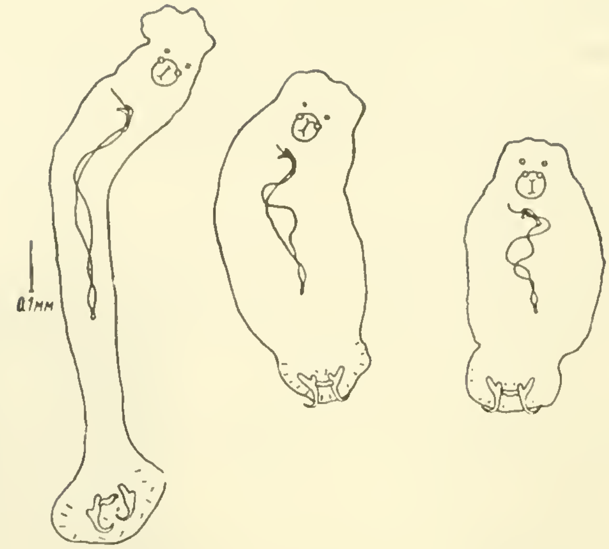

Fig. 3. Dactylogyrus auriculatus (Nordmann), adult worms in various stages of contraction, from gills of Abramis brama (L.) from the Delta of the Volga.

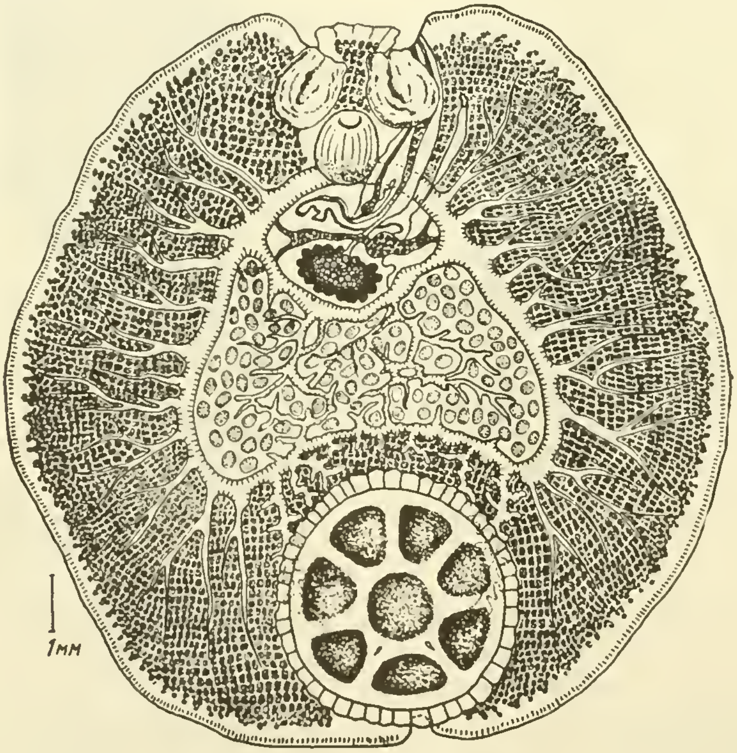

Fig. 4. Tristoma coccineum Cuvier, adult worm from the gills of Xiphias sp. from the region of the Maderia Islands (Atlantic Ocean).

The transverse section of the body (Fig. 10) varies from a rounded shape (as for instance in a series of sections of Dactylogyrus) to one which is greatly flattened dorsoventrally (among representatives of the genus Nitzschia or Capsala). The ventral side of the body is usually slightly concave, and the dorsal correspondingly convex.

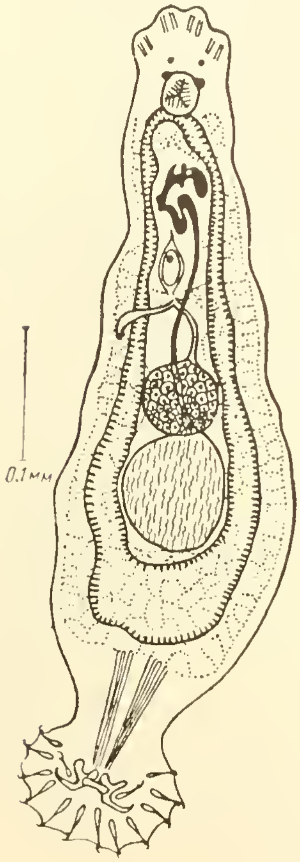

Fig. 5. Dactylogyrus vastator Nybelin, adult worms from the gills of Cyprinus carpio L. from Ropshansk Ponds (Leningrad region) (According to Bychowsky, 1933).

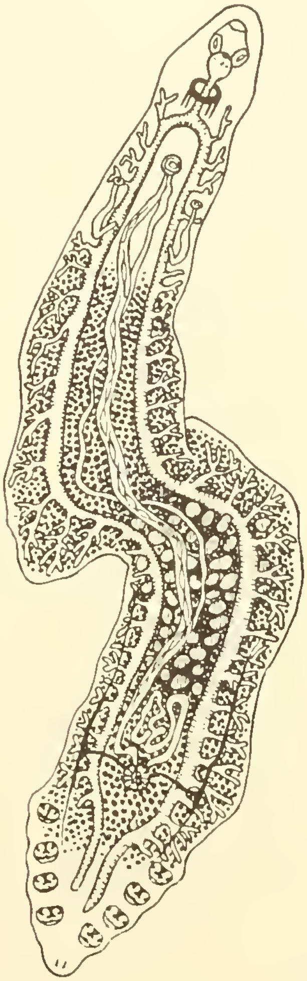

Fig. 6. Vallisia striata Perugia and Parona, adult asymmetrical worm. Natural size 10 mm. (According to Monticelli, 1912).

The lateral sides of the body are entire or smooth with few exceptions (see page 43). This smooth-margined condition does not pertain to the adhesive disc the sides of which can form an intricately cut figure. The orientation of the body of monogenetic trematodes does not offer any difficulty; their oral opening is, as a rule, terminally or subterminally located and the attachment apparatus is always at the posterior end.

Color. The color is usually determined by the color of the internal organs, but the body itself is either colorless or grayish white. Also, thanks to the organs showing through, the color may be rose, reddish, brownish, or even blackish (intestine), milk-white color (vitelline material, p. 15
gonads), yellow color or tan (uterus).

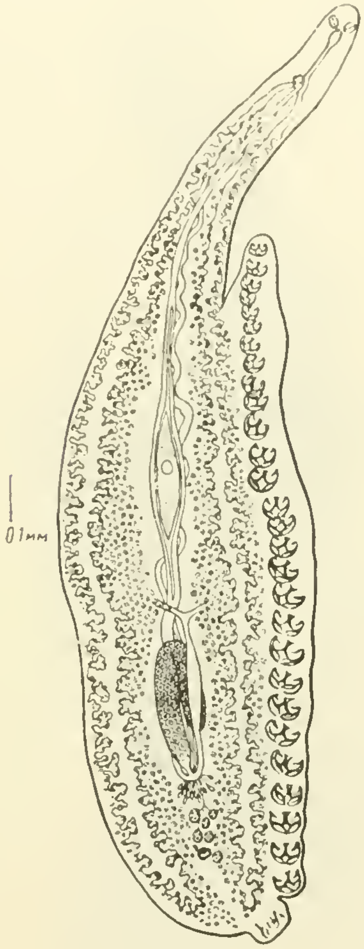

Fig. 7. Gastrocotyle trachuri Beneden and Hesse, adult worm from the gills of Trachurus trachurus (L.) from the region of the Cape Verde Islands (Atlantic Ocean).

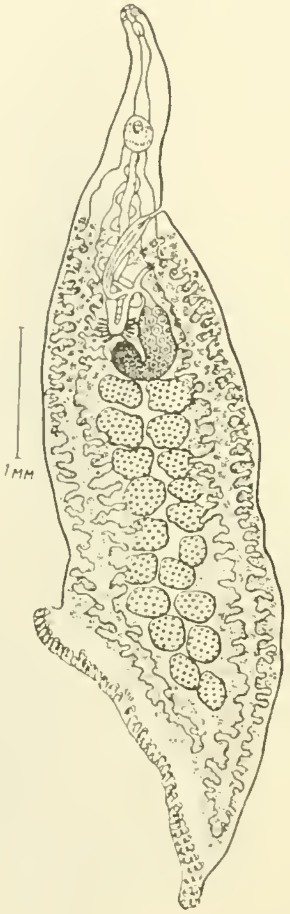

Fig. 8. Axine belones Abildgaard, adult worm from the gills of Belone belone (L.) from the region of Sebastopol (Black Sea)

Attaching Structures. The anterior end of the body bears attaching organs which serve mainly for the attachment of the anterior or head end during feeding, and also play an auxiliary role during the locomotion of the animal. These organs can be divided into two main groups: those that are not connected to the mouth funnel or the oral aperture; and the second type, those that are connected to the mouth funnel or the oral aperture.

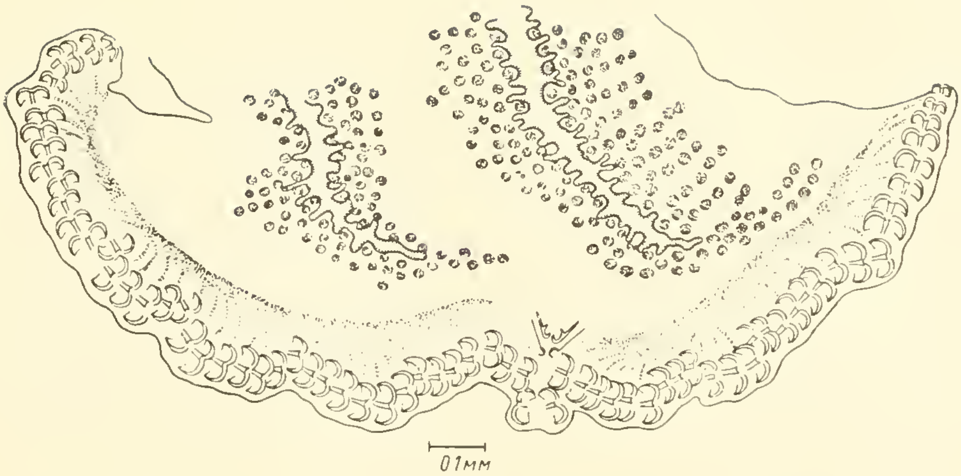

Fig. 9. Axine sp. I, attaching disc (middle hooks of the larval disc are located almost in the middle of the common row of clamps). From the gills of Cypselurus sp. from the region east of the Japanese Islands (Pacific Ocean).

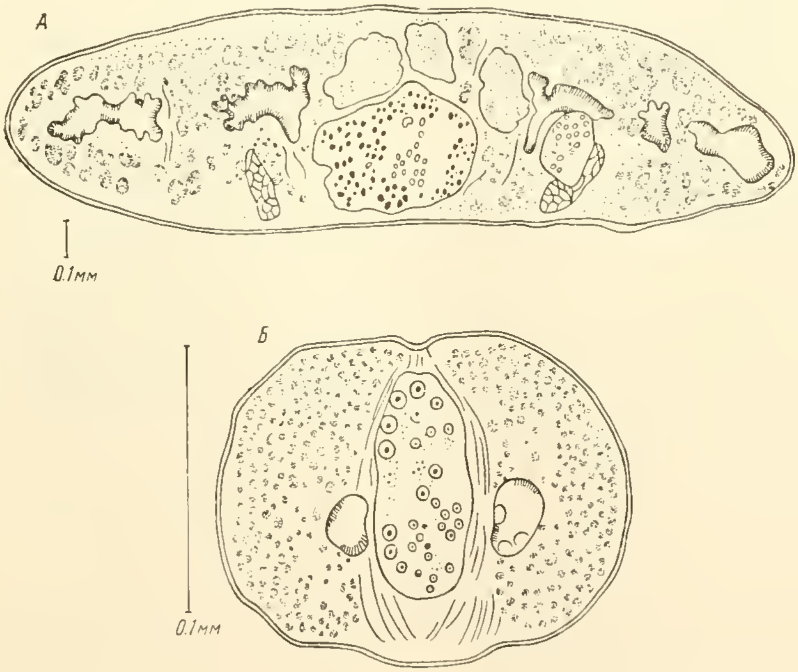

Fig. 10. Cross section of the body of A--Nitzschia sturionis (Abildgaard). B--Ancylodiscoides siluri Zandt.

To the first group of anterior attaching structures are related
the head papillae, the bothria, the little pits and suckers. The second group
includes the buccal funnel, the pharyngeal sucker, and the buccal funnel
suckers. In this connection the anterior end of the most primitive mono-
genetic trematodes is somewhat flattened dorsoventrally, is rounded or p. 16
truncated, and the numerous ducts of the head glands open along its edge,
apparently heterogeneous, but actually producing an agglutinating secretion
which serves for the attachment for the anterior end of the body. In the
majority of cases, in the forms which have as yet no differential growth
of the anterior end of the body, the excretory ducts of the head glands are
not located evenly along the entire anterior edge, but by groups of from
8 to 2 clusters (Fig. 11). In connection with this, we observe in a series
of sections the formation of head organs the anterior end of which are in
the form of more or less well-developed but always moving lobes. The
The number of head glands is usually paired, from one (for instance
Gyrodactylus, Fig. 12) up to 4 (for instance *Murraytrema*, Fig. 13). One
often sees two pairs of head glands (for instance *Dactylogyrinae*, the p. 18
majority of Ancyrocephalinae and others--Fig. 5, 65 and others). Each
head organ receives at its posterior end ducts of the clusters of head glands.
As a rule, one cluster of ducts of head glands enters into one head papilla,
nevertheless sometimes a great number also enter a single head papilla
depending upon an increasing size of the head papillae. The latter, in a
series of cases, develop unequally so that two of them gradually pre- p. 19
dominate and the others disappear (for instance *Diplectanum*, Fig. 14).

Next in complexity of the anterior attaching apparatuses are
the attaching bothria. The latter have the appearance of two thickenings
of the body symmetrically located on the sides of the anterior end and are
weakly separated from it. The musculature of these head bothria is
stronger than that of the head papillae and the head glands open into them
with many individual ducts or by several clusters, (for example *Empruthotrema*, Fig. 15), or equally spaced along its full length (*Dionchus*, Fig. 16).
It is absolutely clear that the head bothria represent the latest stage of
morphological development of the head organs. Further, the process of
complication involves increased musculature of head bothria, and its sepa-
ration from the musculature of the body and the appearance of cup-like in-
dentations on the external side of the bothria, which leads at first to the
formation of head pits (for instance *Nitzschia*, Fig. 17), and also, during
the following development (both in the phylogenesis and ontogenesis) leads
to the formation of more or less strongly developed head suckers (for
instance *Tristoma*, Fig. 4). As a rule there is one pair of head bothria
or suckers (the following present exceptions: 1. The genera *Bothitrema*,
the only species of which *B. bothi* (MacCallum) (Fig. 19) has, judging by
the drawing and description of Price (Price, 1937b), four adhesive pits p. 20
on each side of the anterior end (see however page 396); and secondly,
the genera *Loimos* and *Loimosina* (Fig. 20) in which the anterior end has
four small head suckers. As for the head glands in adult forms, the

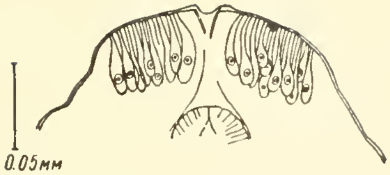

Fig. 11. Head end of the larva of an undetermined monogenetic trematode from the gills of *Prognichtis agoo* (Schl.) near the Banks of Hokkaido (Pacific Ocean).

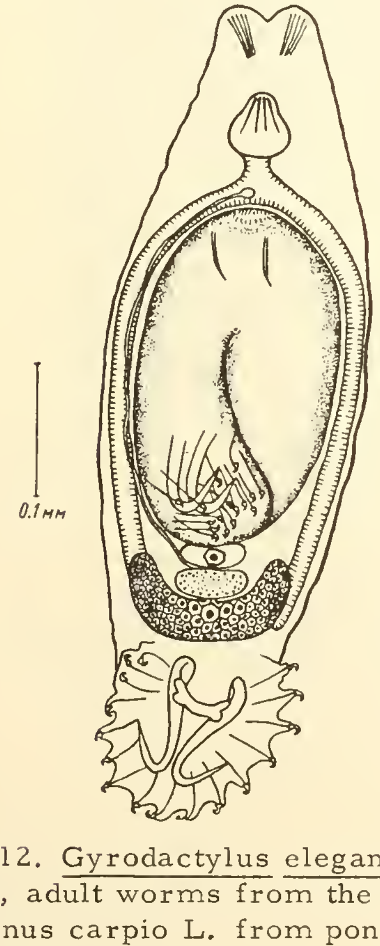

Fig. 12. *Gyrodactylus elegans* Nordmann, adult worms from the gills of *Cyprinus carpio* L. from pond farms in the region of Alma-ata (Kazak, SSSR).

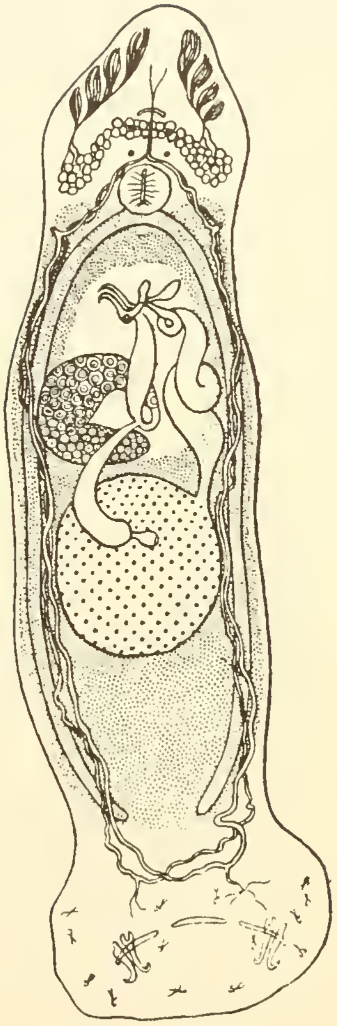

Fig. 13. *Murraytrema robustum* (Murray), adult worm. Natural size 2.5 mm (According to Murray, 1931).

number decreases in proportion to the complication of the muscular attaching apparatuses (concerning the ones that are still developing, see the corresponding section of the book).

The second group of anterior attaching structures, as has been stated above, is associated with the oral aperture and the buccal funnel.

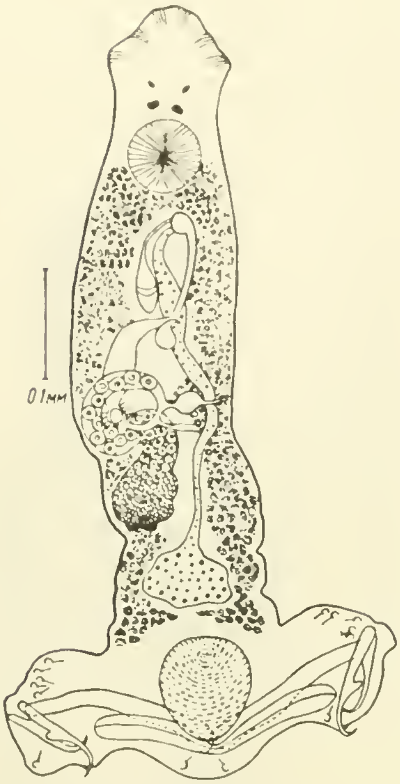

Fig. 14. *Diplectanum similis* Bychowsky, adult worm from the gills of *Corvina nigra* Cuv. and Val. from the region of Karadaga (Black Sea).

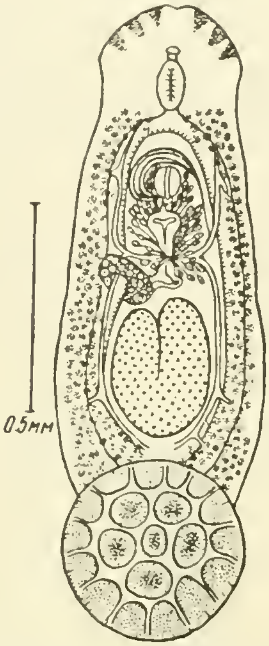

Fig. 15. *Empruthotrema raiae* (MacCallum), adult worm. (According to Price 1938)

Actually, we deal with two separate structures, to be more precise with the changes in shape of the anterior end of the buccal funnel and with its suckers.

In the simplest case the external edge of the buccal funnel serves for adhesion (for example *Linguadactyle*, Fig. 21). Further, we have all stages of transition to the formation of a more or less well-developed oral p. 21 sucker around the oral orifice at the expense of the buccal funnel *Squaloncho-cotyle*, Fig. 2; *Polystoma*, Fig. 22). Apparently in unusual cases one of the edges of the mouth sucker can form a series a series of sucking pits, but in no case do they represent the transitional link to the following group. In other cases in which there are no changes in the external edge of the buccal funnel, which remains in its primitive state, on the internal surface of the funnel along its sides there begin to form two internal suckers which in various species reach differing degrees of attaching capabilities (Figs. 23, 24). These suckers of the buccal funnel are not connected in origin with the other

head structures which serve for attachment, but represent formations peculiar to a large group of families of monogenetic trematodes Diclido- p. 22
phoridae, Mazocraeidae, Microcotylidae, etc., see the systematic section, page 402. One must note that in the work of Braun, mentioned in the
beginning of this chapter, the author points to the principal distinction between the first and second groups of the attachment organs of the anterior
end of the body of these animals, saying that the former and the latter are
in no way linked genetically, because some of them appear as derivatives p. 23

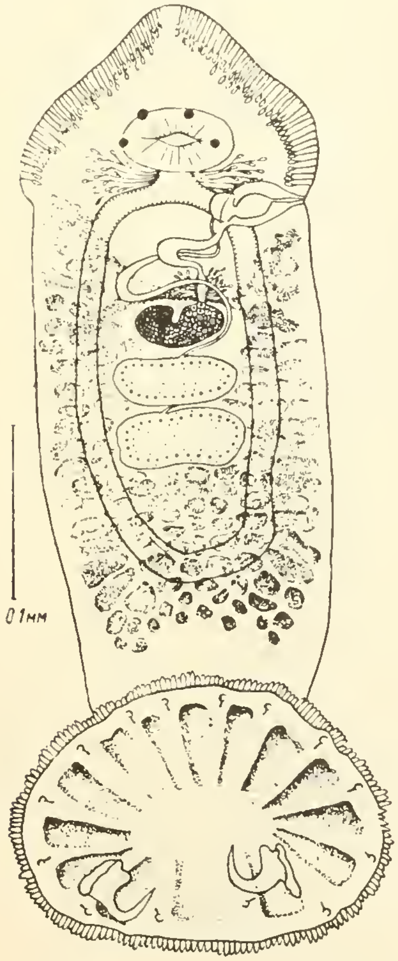

Fig. 16. Dionchus agassizi Goto, young worm from the gills of Remora remora (L.) from the Indian Ocean.

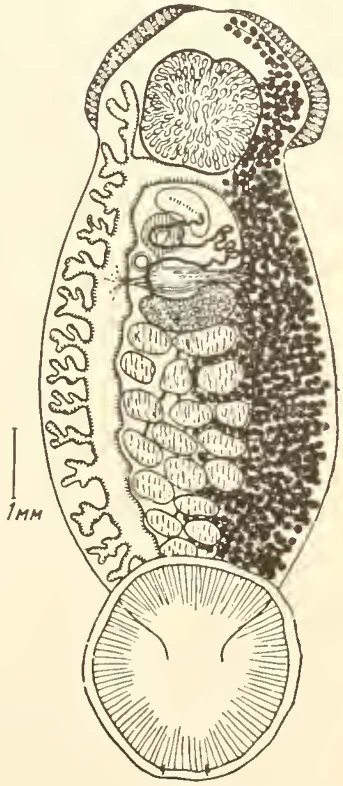

Fig. 17. Nitzschia sturionis (Abildgaard), adult worm from the buccal cavity of Huso huso (L.) Island of Sara (Caspian Sea).

of the exterior layers and others appear as derivatives of the layers limiting the buccal cavity. Unfortunately, this direct statement of Braun has not been sufficiently taken into consideration by specialists in the group and this oversight has led to completely arbitrary and wrong conclusions concerning the interrelations of the different systematic groups.

In order to complete the description of the anterior attaching apparatus, one must also note that the species that have apparatuses of the second type are also equipped with head glands which open by their ducts on the anterior edge of the body in a varying number of clusters, but independently of the buccal funnel and its derivatives. Thus, in *Microcotyle* they open by three clusters of ducts (in front and along the sides of the buccal funnel), in *Octostoma* by two clusters of ducts, etc. (see Fig. 23 and also the chapter on embryology).

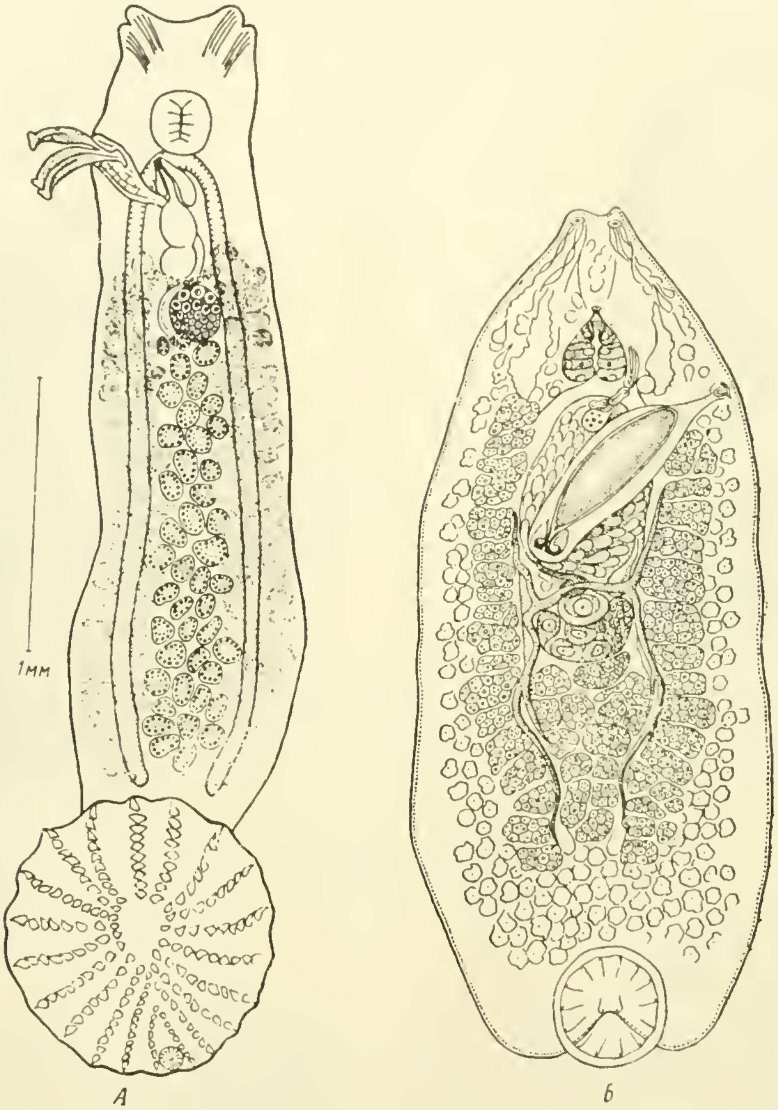

Fig. 18. A. *Acanthocotyle williamsi* Price, adult worm from the skin of *Raja rosispinus* G. and Town, near the eastern region of southern Sakhalin (Sea of Okhotsk); B. *Enoplocotyle minima* Tagliani, adult worm. (According to Tagliani, 1912). Natural size 0.4 mm.

Attaching Disc. The main attaching apparatus which is used for the fixation of the animal to the body of its host is a complexly arranged system of attachment organs lying on the posterior end of the body, which sometimes extends for a considerable distance anteriorly. This system consists of the adhesive disc and of the different attaching organs located thereon (Fig. 25). The adhesive disc varies in its structure in a series of cases, also in its origin. We can distinguish discs weakly or strongly delineated from the rest of the body and, finally, primary and secondary

p. 2

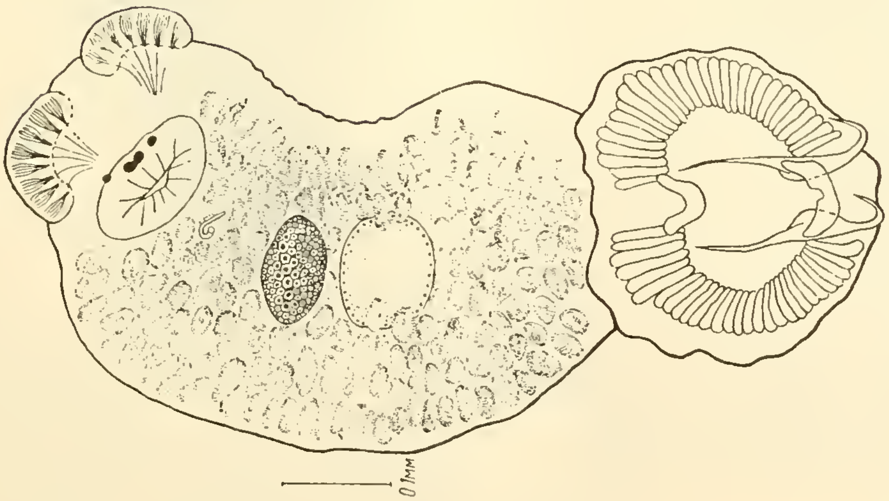

Fig. 19. *Bothitrema bothi* (MacCallum), adult sample from the gills of *Lophopsetta maculata* (Mitch.) from the region of Woods Hole (Atlantic Ocean).

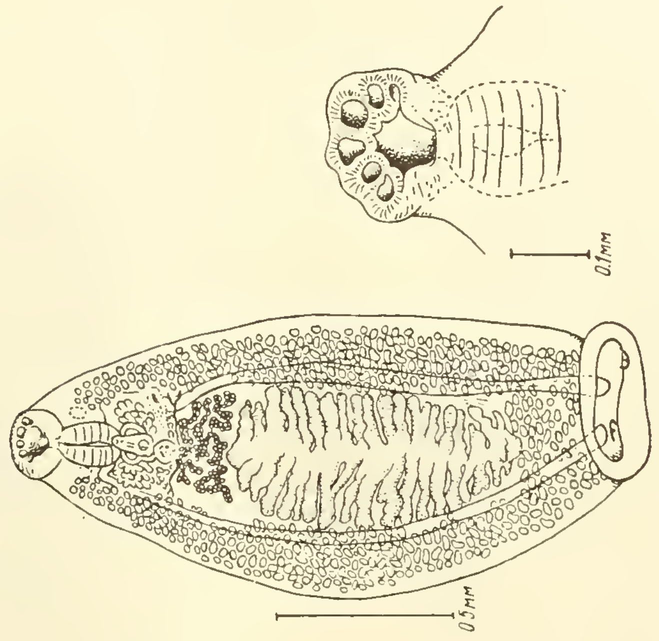

Fig. 20. *Loimosina wilsoni* Manter, to the left--adult worm, to the right--its head end. (According to Manter, (1944).

ones which are not homologous to each other. In itself the attaching disc
represents, even in the most primitive state, an organ of attachment
similar to the corresponding developments of the posterior end of certain p. 25
Rhabdocoela. It is usually equipped with a series of powerfully developed
agglutinating glands (see below). However, one must note that in certain
groups the attaching disc of the adult monogenetic trematode ceases to fulfill the functions of attachment, abandoning this function to attaching organs
which are placed upon it.

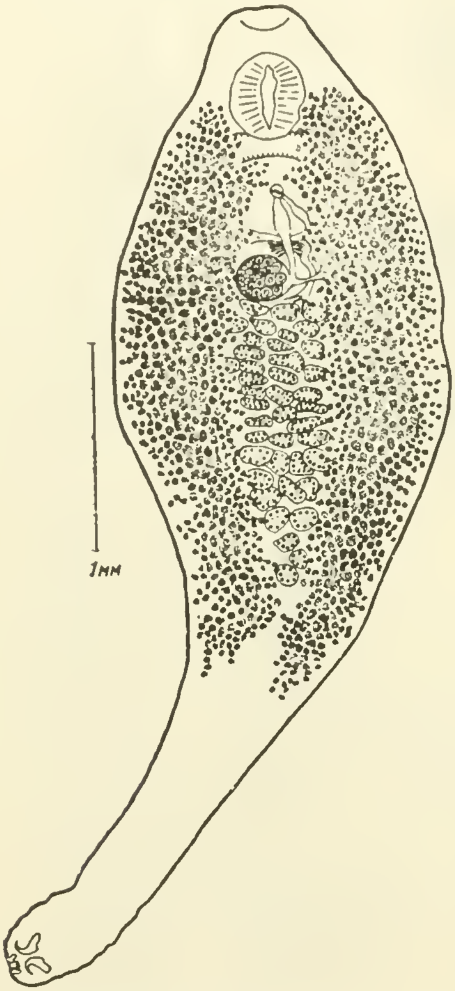

Fig. 21. Linguadactyla molvae Brinkmann, adult from the gills of Molva dipterygia elongata (Otto) near the shores of Spain (Atlantic Ocean).

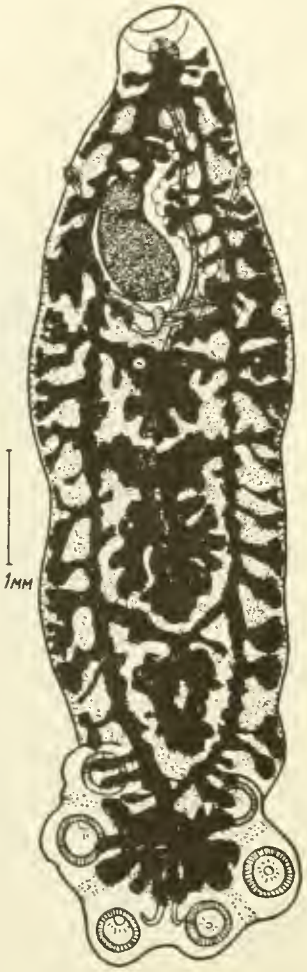

Fig. 22. Polystoma integerrimum Froelich, adult worm from the urinary bladder of Rana temporaria L. from Peterhof (Leningrad region).

The most primitive is the disc which is weakly delineated from the body, and in actuality represents a direct continuation of the body. Usually such a type of disc is somewhat flattened in comparison with the rest of the body, and in this connection is somewhat more muscular. Examples of such a disc can be seen in Protogyrodactylidae (Fig. 26), and in the majority of Dactylogyridae (Fig. 5). As a counterpart to such discs could be considered those that are bound together by numerous connecting ridges and which are sharply delineated from the rest of the body, and which are powerfully developed for the sucking action, as in Monocotylidae (Fig. 27) and Capsalidae (Fig. 1). Discs of such a type can be very complicated. In them is developed a very complicated series of muscular fibers which is often completely isolated from the main musculature of the body. The cuticle of the outer edge of such sucking discs forms a very thin membranous margin which is usually entire throughout (for instance *Nitzschia*, Fig. 17) or cut into festoons (as in *Trochopus*, Fig. 28). Various

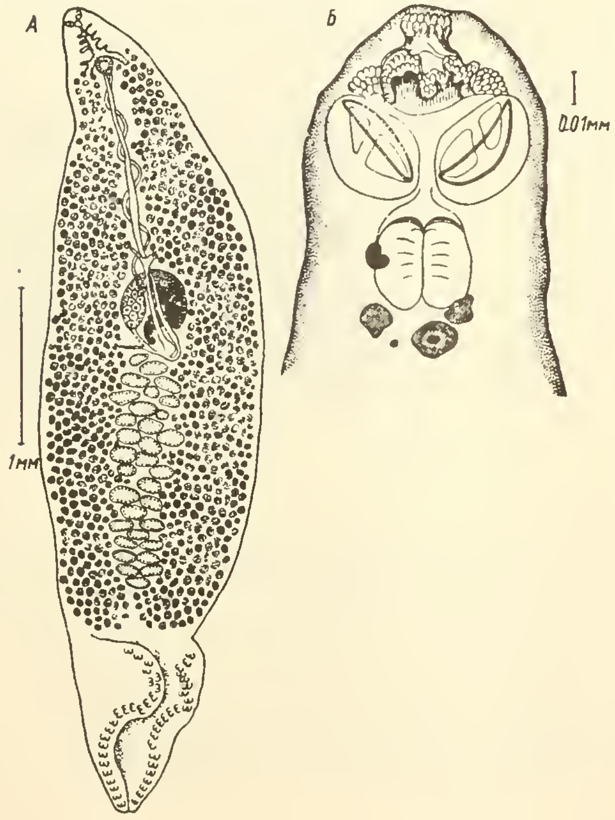

Fig. 23. *Microcotyle* sp. sp.: A--*M. mugilis* Vogt, adult worm from the gills of *Mugil auratus* Risso from Sebastopol Bay (Black Sea); B--*M. gotoi* Yamaguti, anterior end of the body (head glands!) of the adult worm from the gills of *Hexagrammos octogrammus* (Pal.) from the region of Yablochnoii (Southern Sakhalin, Sea of Japan).

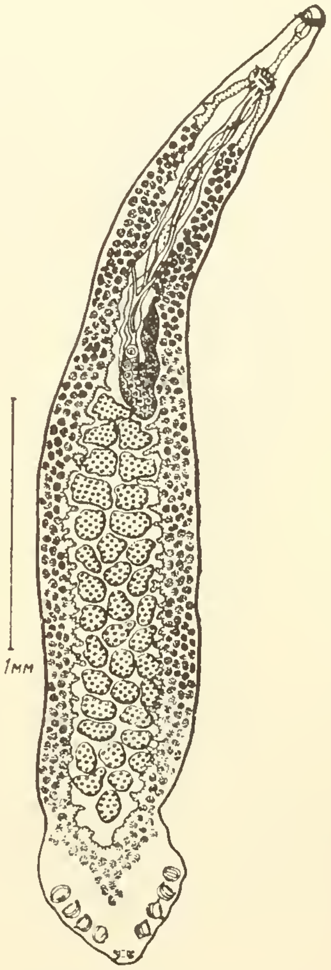

Fig. 24. *Mazocraes alosae* Hermann, adult worm from the gills of *Alosa caspia* (Eichw.) near the Island of Sara (Caspian Sea).

muscular partitions arranged in a more or less complicated fashion are formed on the internal surface of such attaching discs, among many species (Trochopus, Fig. 28, Capsala, Fig. 1). The main part of the suction discs p. 26
have a precisely rounded form, and in rare cases are laterally elongated (as for instance, Tetraonchoides, Fig. 29) or longitudinally elongated (for example, Thaumatocotyle, Fig. 30).

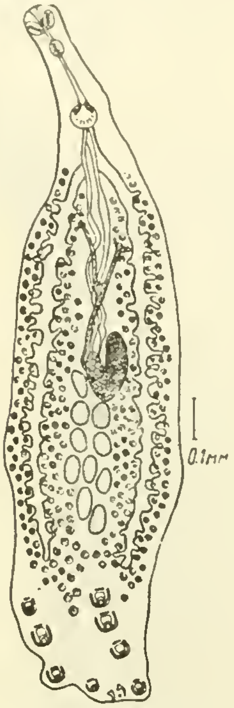

Fig. 25. Octostoma minor (Goto), adult worm with weakly developed attaching disc, from the gills of Pneumatophorus japonicus (Hout.) from the region Yablochnoii (Southern Sakhalin, Sea of Japan).

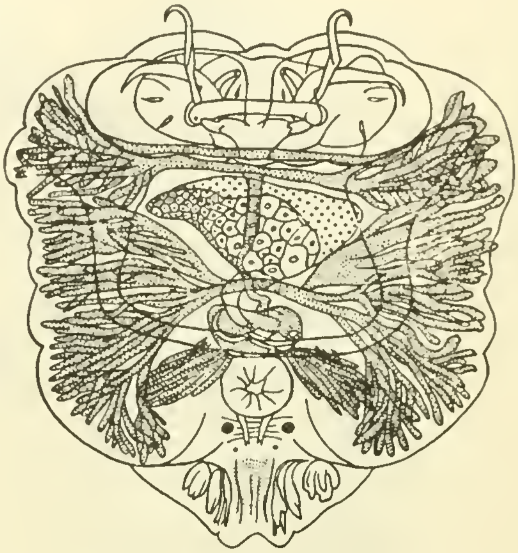

Fig. 26. Protogyrodactylus quadratus Johnston and Tiegs, adult worm, size is about 0.23 mm. The worm contracted strongly during fixation, apparently in normal condition it is more elongated. (According to Johnston and Tiegs, 1922).

The following group of discs, not less well-delineated from the body, and likewise supplied with a powerful musculature, but lacking the suctorial form, is similar to the second type which was described. This group is typical for the monogenetic trematodes in that the organs located on the ventral side or along the sides of the disc are the main or basic organs of attachment.

One must note that the form of the disc can fluctuate considerably from round to very elongate, while the edge of the disc changes from the equally round one to a highly indented one. Often the disc forms paired and odd growths of different extent, as a rule they are symmetrically arranged. The discs of Polystomatidae (Fig. 22) and Hexobothriidae (Fig. 2) can be considered as samples of discs of this type. Here also can be placed the disc of Microcotylidae (Fig. 23) which, nevertheless, differs in its structure, on the one hand in connection with the asymmetry of the disc in a number p. 27 of forms as for instance (*Axine*, Fig. 9) and on the other hand, as a result of more complex relations with the body of the animal (see page 439). Finally, the discs of Acanthocotylidae (Fig. 18,A) represent the last group of attaching discs which have a secondary origin, while the primary disc remains non-functional, lying on the secondary one (see page 383).

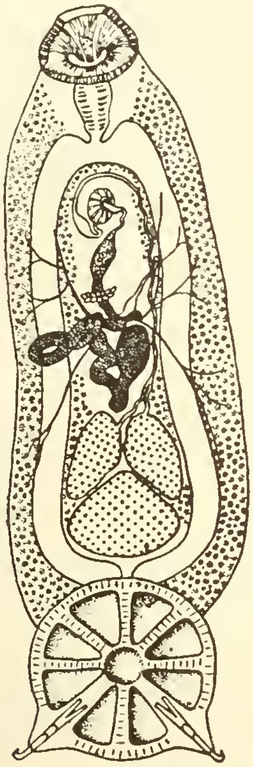

Fig. 27. *Monocotyle myliobatis* Taschenberg, adult worm. Magnified 20 times. (According to Palombi, 1942).

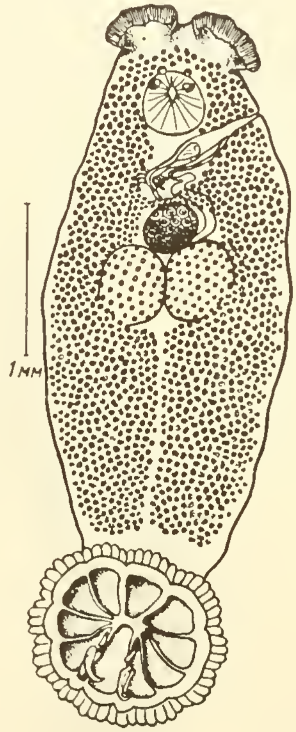

Fig. 28. *Trochopus pini* (Beneden and Hesse), adult worms from the gills of *Trigla lucerna* L. from the Bay of Biscay (Atlantic Ocean).

The attaching organs lying on the disc can be divided into groups of chitinous[1] and muscular formations; however, the latter are not encountered, or more precisely, are encountered very rarely outside of their connections with the chitinous organs. As a result of this, it is more convenient to group the attaching organs as a whole, that is by the combination of separate parts, which form an independently functioning unit. Systematizing in accordance with this principle we obtain four basic groups, specifically: a group of hook-shaped organs, a group of supplementary discs with chitinous armature, a group of suckers, and p. 28 a group of attaching valves. Let us immediately note that the same species of animal can have attaching organs of one, two, or three types.

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[1] As regards the term "chitinous" we must explain that by this term is meant the physical consistency of the formations and not their chemical constituency because at the present time this has not been elucidated. Our own efforts to do this were unsuccessful.

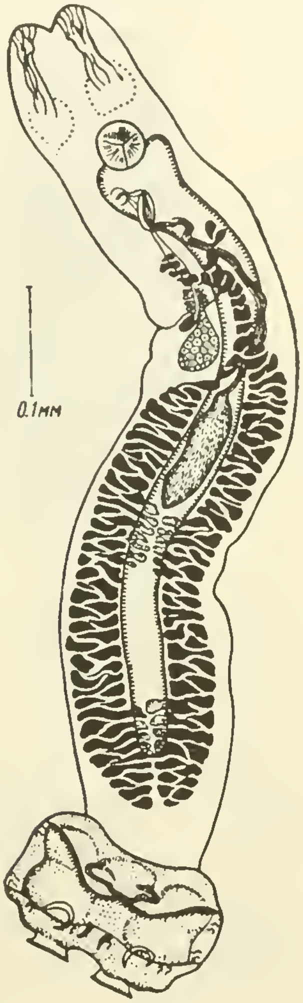

Fig. 29. Tetraonchoides paradoxus Bychowsky, adult worm from the gills of Uranoscopus scaber L. from the Bay of Sebastopol (Black Sea).

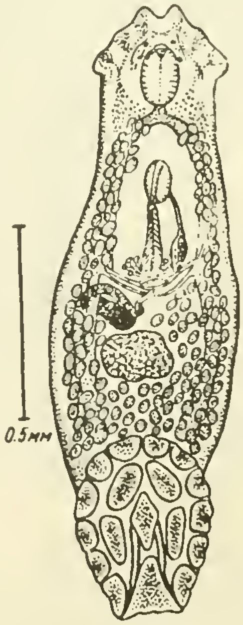

Fig. 30. Thaumatocotyle dasybatis (MacCallum), adult worm. (According to Price, 1938).

The first group, that is the hook-shaped organs, is the most widespread. It is represented by chitinous structures of a very different shape and size and by different chitinous parts which connect or support the hooks, and also the attaching disc itself. Chitinous hooks are subdivided into the edge type and central type.

The edge hooks (Fig. 31) at first are located along the periphery of the disc whence they receive their name; however, as will be stated later, in a number of species and groups they can also be located on its central surface. The structure and sizes of edge hooks vary. In the typical case the edge hook is divided into two basic parts, the first is the parenthesis or sickle-shaped edge hook with a sharpened free end and with a handle extending from the top end of the curved part of the end hook in the shape of a differently arranged stem. For the most part, a lateral growth which appears as if it were constructed of the end of the end hook and the beginning of handle lies between these sections or two parts. Among many forms (for instance Polystomatidae and Microcotylidae) there is a special loop or structure near the end hook which lies at the lower part of the hook and through which it extends. We will consider this formation in connection with the fact that it plays a specific role during the formation of the attaching valves (see also page 407). The number of edge hooks hooks in various groups varies, usually it fluctuates between 16 and 10, or to be more precise from 8 to 5 pairs for as a rule they are symmetrically located on the disc. In certain cases the number of edge hooks is smaller in connection with the disappearance of part at the time of the postembryonic development (as for instance Microcotylidae, see page 212).

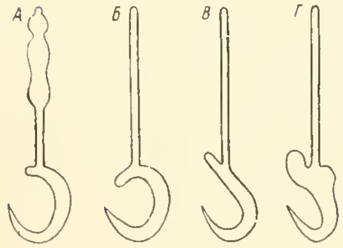

Fig. 31. Marginal hooks:
A--dactylogyrid type;
B--gyrodactylid type;
C--octocotylid type; and
D--polystomatid type
(Schematically).

Middle hooks (Fig. 32), as their name indicates, are primarily located in the center of the attaching disc, and later in a number of forms (just as in orthogenesis, also in phylogenesis) they can be displaced to the posterior end or the sides of the disc. In a typical case the middle hook represents an elongated plate sharpened at one end and forming two growths (continuations) on the opposite end, bent in one flat area in such a way that its sharpened end lies much closer to the inner growth than to the outer growth. The correlation between the growths in the basic parts and the point are very different just as the size of the entire hook varies. Sometimes the middle hooks have another form different from the typical one, but which is similar in form to the edge hooks. In the latter case their origin is usually not clear, and it is possible that we are dealing here with altered edge hooks which are not homologous to the middle hooks themselves (see chapter on embryology, page 101). Between the middle hooks, various chitinous bars can be located (Fig. 33) which serve to link the middle hooks, and also for the attachment of the musculature of the latter and for fastening p. 29

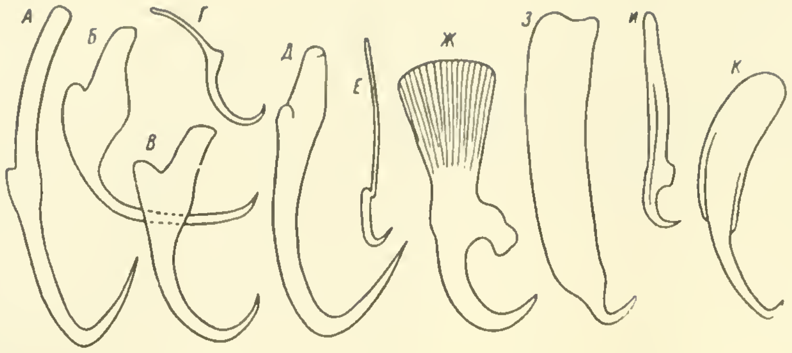

Fig. 32. Different types of middle hooks of A--*Dactylogyrus anchoratus* (Dujardin); B--*D. alatus* Linstow; C--*D. wunderi* Bychowsky; D--*Mazocraes alosae* Hermann; E--*Gyrodactylus medius* Kathariner; (from the first pair) F--*Diplozoon paradoxum* Nordmann; G--*Octostoma scombri* Kuhn (from the second pair); H--*Nitzchia sturionis* (Abildgaard) (from the third pair); I--*Dasybatotrema dasybatis* (MacCallum); J--*Thaumatocotyle dasybatis* MacCallum. The sizes in relation to each other are disregarded.

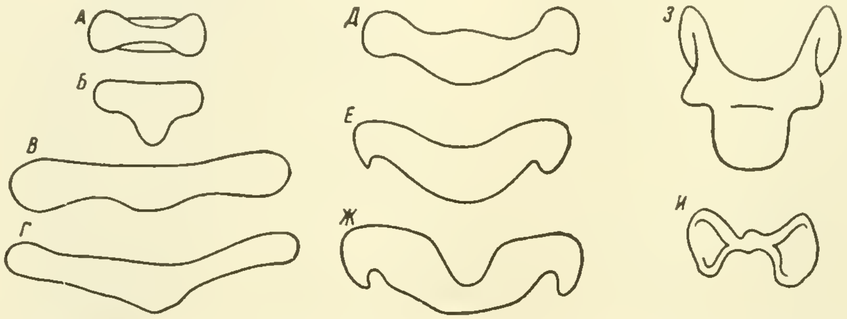

Fig. 33. Different types of connecting plates of the middle hooks. A--*Dactylogyrus anchoratus* (Dujardin); B--*D. simplicimalleata* Bychowsky; C--*D. drjagni* Bychowski; D--*D. longicopula* Bychowski; E--*D. cryptomeres* Bychowski; F--*D. wunderi* Bychowsky; G--*D. kulwieci* Bychowsky; H--*Gyrodactylus arcuatus* Bychowski; I--*Tetraonchus monenteron* (Wagener).

them to the attaching disc itself. The shape, the sizes, the number and their relative position are varied. Among various forms the number of middle hooks can fluctuate from one pair up to three pairs (just as edge hooks, basically this is a symmetrically arranged formation). Middle hooks can also be absent (as for instance in *Acolpenteron*, Fig. 44).

The second group, that is supplementary (or compensating discs), is represented by the following disc-shaped growths or organs which lie one by one on the ventral surface of the disc. They are located on the attaching discs in front of the middle hooks and the apparatus which joins them. Each one of these growths is equipped with special musculature which allows it to change its size and degree of convexity and is also equipped with chitinous concentric rings (Lamellodiscus, Fig. 34) or concentric p. 30
rows of individual chitinous straight spines (Diplectanum, Fig. 14) which serve for the process of attachment along with the system of lateral and middle hooks.

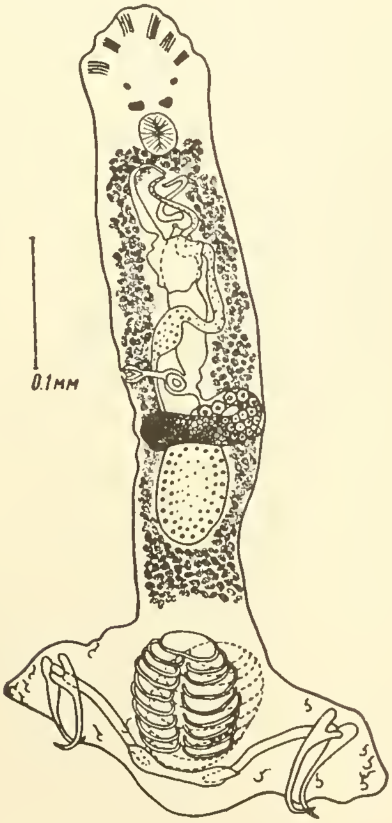

Fig. 34. Lamellodiscus elegans Bychowsky, adult worm from the gills of Sargus annularis (L.) from the region of Karadaga (Black Sea).

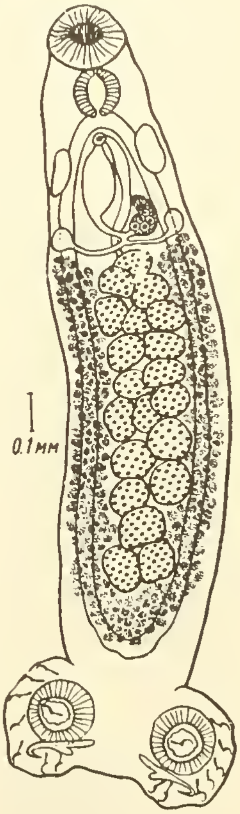

Fig. 35. Sphyranura osleri Wright, adult worm from the skin of Necturus sp. from the Huron River, (Michigan, U.S.A.).

The secondary disc of Acanthocotyle (Fig. 18, A) which replaces the primary attaching organs functionally (see pp. 36 and 383) has a structure similar to the secondary discs of Diplectanum.

The third group of attaching organs, that is of suckers, does not require a detailed description.

The suckers are basically of one structural type differing from each other in shape and size, and also by the presence of subdivisions within themselves and as a rule various chitinous formations which are derivatives of the lateral hooks.

The number of suckers usually fluctuates from 2 to 8, and they are located symmetrically along the ventral surface of the attaching discs (Figs. 22, 35, 36). p. 31

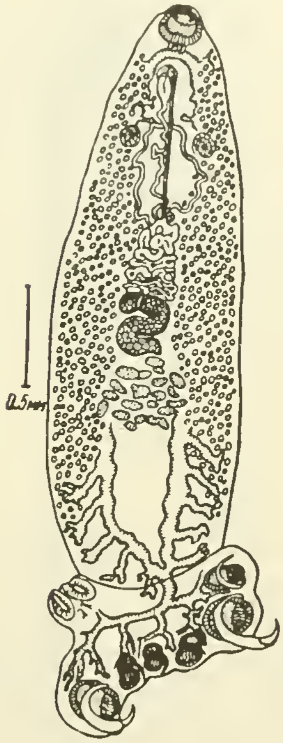

Fig. 36. Heteronchocotyle hypoprioni Brooks, adult worm, (According to Brooks, 1934).

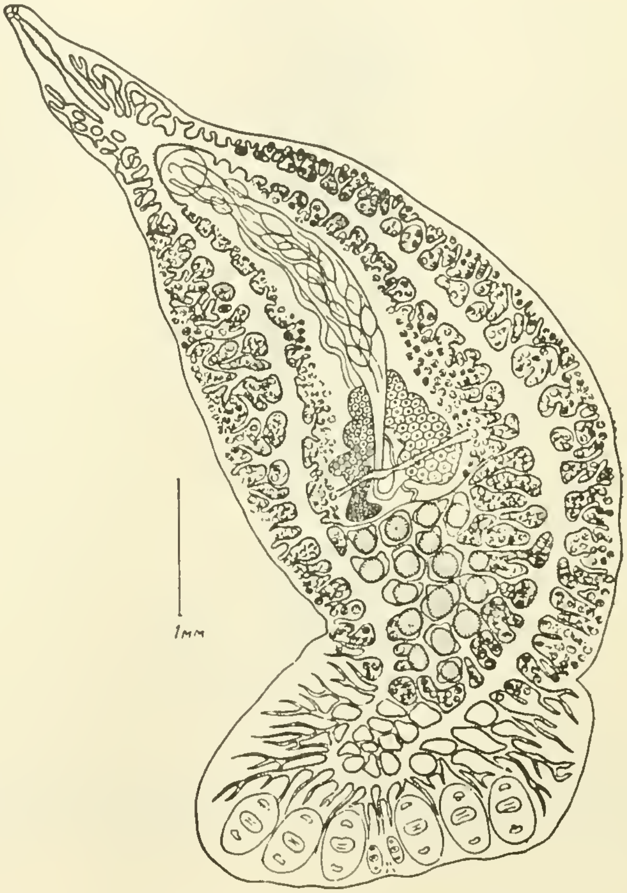

Fig. 37. Hexostoma grossum (Goto), adult worm from the gills of Katsuwonus vagans (Less.) from the region Nagasaki (East China Sea).

To this group are related the special suction-type formations of the attaching discs among representatives of Tetraonchoididae (Fig. 29). They are arranged by two pairs on the dorsal surface of the posterior part of the disc so that the first pair is located almost in the middle of the longitudinal axis of the discs, symmetrically along the sides of the longitudinal axis; and the second pair lies in the same fashion, but nearer the posterior end of the disc. These suction-type formations are in the shape of little round pillows which stand out on the surface of the disc, each one of them bears a very weakly noticeable chitinous, sickle-type plate.

The fourth, that is the group of attaching clamps, is characteristic of the highest types of monogenetic trematodes. The attaching clamps represent a complex system which arises from a muscular sucker and the powerfully developed chitinous parts; with this on the one hand we can observe forms in which the muscular part predominates, and on the other hand forms with a preponderance of chitinous formations. In the latter case we cannot even mention the word sucker, because this apparatus p. 32
functions not as a suction mechanism but as a pinching mechanism. One can observe numerous transitions between the extreme forms which were mentioned. Attaching valves among Hexostomatidae[1] have (Fig. 37) the most primitive structures which represent almost a typical sucker with three chitinous parts, of which one is X-shaped, and lies in the middle in the special muscular partition which separates the sucker (clamps, nobis) into right and left halves and two others of irregular shape are located on the right and left edges. If you can imagine now that the sucker (clamp, nobis) of such a type will be constructed along the cross axis, then we will obtain the following morphological stage and actually the first real attaching clamp, principally distinguishing itself from the suckers in having ventral and dorsal clamp halves or valves (Fig. 38).

The subsequent complication (or evolution, nobis) proceeds along the lines of an increase in the number and sizes of chitinous parts. In the typical attaching clamp (Fig. 39) we can distinguish two parts corresponding in origin to the right and left halves of the initial suction type; at the same time, a greater part of the chitinous armature of one half is larger and of a somewhat different shape than that of the other. We can consider as the most widespread type of clamp the type with its chitinous parts situated in the following way: The largest band (Bychowsky uses plate in place of band throughout, western workers employ the word sclerite, nobis) lies along the longitudinal axis, that is across the clamp,

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[1] It must be noted that the morphological primitiveness of the clamps of Hexostomatidae appears to be a result of secondary simplification; on very careful analysis this primitiveness is only illusory (see page 421).

and extending into both of its valves and representing a spring, so to speak, now bending, now straightening. In each half of the clamp along the sides of the valves lies one curved band as if supporting the edge. These four bands lie in such a way that at the place of junction of both halves of the clamp they articulate in pairs from each side so that the corresponding bands of both clamp halves or valves articulate with each other. Their free ends extend along the edge of the valve and reach under the ends of the middle band. At the place of articulation of each two lateral bands lies one (usually short) band which unites with them and with its free end extending toward the middle band along the outer surface of the dorsal clamp of the valve. For the most part, the middle band p. 33
is linked to the others by special growth or organs in the places of their articulation. From those which have such structure of attaching clamps result, on the one hand, the types which distinguish themselves by the complication of form as well as by the increase in the number of chitinous parts, and on the other hand simplified attaching valves in which chitinous details disappear.[1] As a rule the attaching valves are located symmetrically on the disc (for instance *Microcotyle*, Fig. 23), however, in a number of cases there are fewer on one side of the disc (for instance *Heteraxine*, Fig. 40) or they are totally absent (for instance *Gastrocotyle*, Fig. 7), which, in this connection, leads to the formation of asymmetrical attaching discs. The formation of asymmetrical discs armed with valves can originate in two ways. In the first, apparently the more widespread asymmetry results by the way of formation of an increasingly smaller number of valves on the one side of the disc up to cessation of their inception altogether during the time of development. With

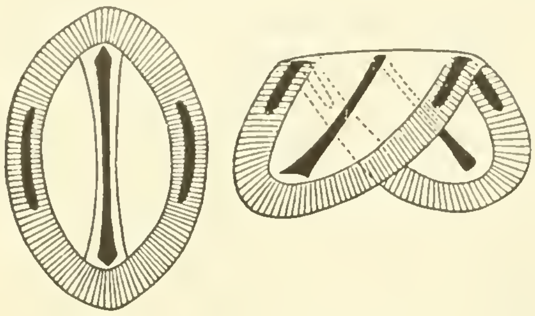

Fig. 38. Diagram of the structure of the primitive attaching clamp. On the left the clamp is fully open, on the right--it is partially closed. The chitinous parts are in black, the musculature is cross-hatched.

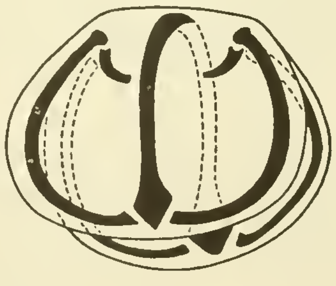

Fig. 39. Typical attaching clamp. Explanation in text.

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[1] The details about this appear in the chapter "Taxonomic System of Monogenetic Trematodes" (pages 416 to 447).

this, the middle hooks of the disc remain on its posterior end (Heteraxine). The second type of asymmetry results in more or less equal numbers of valves on both sides of the middle hooks in such a way that the right side of the disc with its attaching clamps performs, so to speak, a movement or motion with the middle hook as a pivot point, thus establishing a single line of clamps with the left half. The final result is a straight line of clamps with the middle hooks located in the middle and at a sharp angle to the longitudinal axis of the body of the animal (Axine, Fig. 9). The question relative to the formation of asymmetrical discs is studied in detail, although very briefly, in the work of U. A. Strelkow (1953). The number of clamps usually varies from eight to several hundred. The sizes in one individual are more or less the same, although there are species in which some of the clamps are much larger than p. 34 the others (e.g. Pseudoanthocotyle, Anthocotyle, Figs. 41, 42).

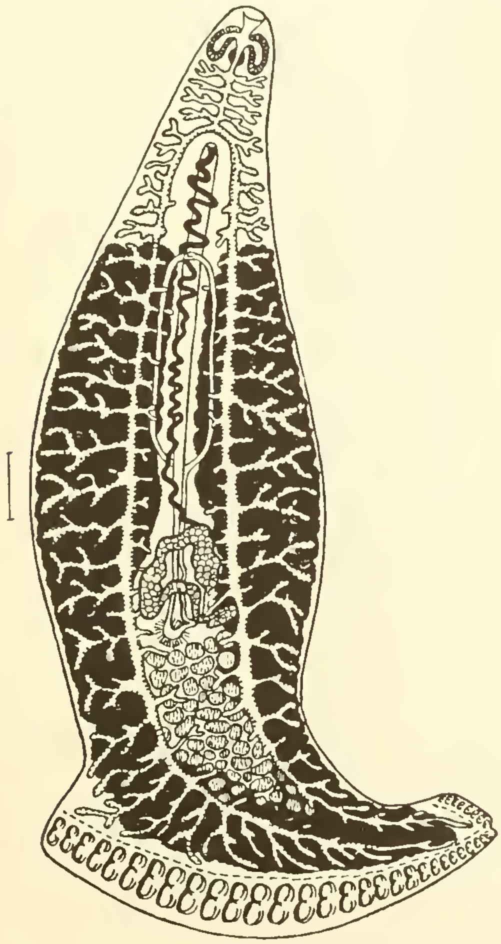

Fig. 40. Heteraxine heterocera (Goto) adult worm. The size of the little line indicates the natural size of the worm. (According to Goto 1894).

The correlation between different types of attaching formations in the various groups of monogenetic trematodes is not the same.

Gyrodactylidae, Protogyrodactylidae, Dactylogyridae, Amphibdellatidae and Tetraonchidae have only chitinous attaching apparatuses. The disc of these forms is more or less strongly delineated from the body and it is flat or concave; but not suction type. Lateral and middle hooks are located on the disc. In some instances, middle hooks are absent (in the genera Isancistrum, Fig. 43; Acolpenteron, Fig. 44; Anonchohaptor, Fig. 45). Wherever they exist, chitinous joining apparatuses are also usually evident with the hooks, nevertheless, there are forms with middle hooks but without joining plates (for instance, Protancyrocephalus, Fig. 46).

In addition to the middle and lateral hooks and connecting plates, the Diplectanidae also have disc-like growths on the dorsal and ventral surfaces of the disc (see page 355). The attaching apparatus of Tetraonchoididae (page 394) and Bothitrematidae (page 395) is more complexly arranged. p. 35

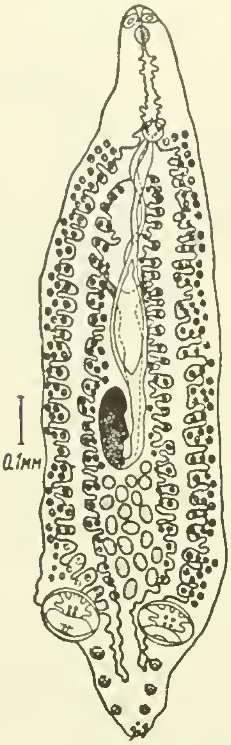

Fig. 41. *Pseudoanthocotyle pavlovskyi* Bychowsky and Nagibina, adult worm from the gills of *Scomber canagurta* Rupp. from the region of the Island Liu-Kiu (East China Sea) (According to Bychowsky and Nagibina, 1954).

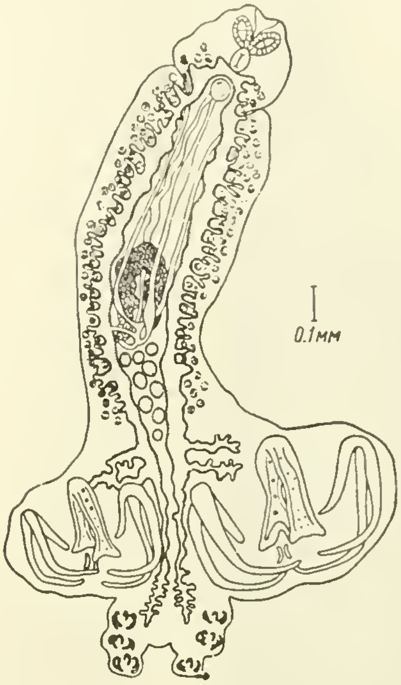

Fig. 42. *Anthocotyle merlucii* Benedene and Hesse, adult but not fully matured worm from the gills of *Merluccius merluccius* (L.) near the western shores of England (Atlantic Ocean) (According to Bychowsky and Nagibina, 1954).

Among Calceostomatidae, Monocotylidae, Loimoidae, Dionchidae and Capsalidae the attaching disc represents a more or less developed, well-delineated sucker also provided with lateral and middle hooks as in the previous families. (Calceostomatidae have one pair of middle hooks and twelve edge hooks on their discs.) Their disc is powerfully developed and provided with a festoon-shaped cutout fringe. Among Monocotylidae there is one genotype (*Empruthotrema raiae* MacCallum, Fig. 15) which is devoid of middle hooks whereas all the remaining species have one pair of middle hooks and 14 edge hooks. As a rule there is no chitinous connecting apparatus. Genera of this family have varying numbers of partitions or septa which separate the suckers into a series of isolated attaching alveoli on the attaching disc, the number of these alveoli varies greatly. Usually there is one lying in the center and from 7 to 100 or more laterally located symmetrically in relation to the longitudinal axis of the attaching disc

(Figs. 47, 48). Capsalidae have from one to three pairs of middle hooks and fourteen edge hooks. Likewise, among Monocotylidae the disc is divided into parts by septa in a number of genera. Among Capsalidae and closely related genera there are seven septa (Fig. 1) and in the genus Trochopus there are ten (Fig. 28). The septa are located in the same fashion as Monocotylidae forming a central alveolus and peripheral alveoli (corre- p. 36 sponding to the number of septa -- 7 or 10). The trimming of the disc is the same as in Monocotylidae and also in Capsalidae.

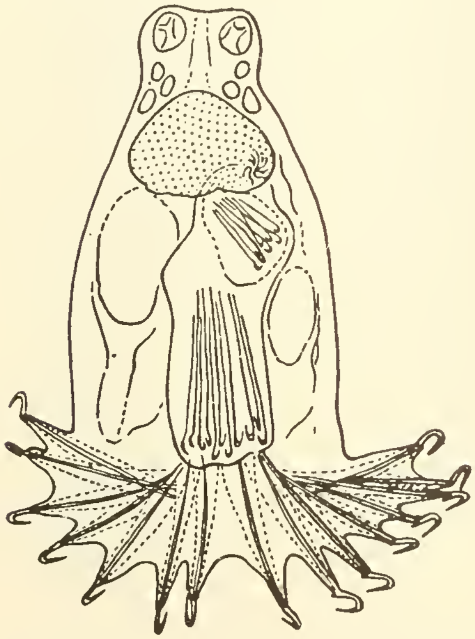

Fig. 43. Isancistrum loliginis Beauchamp, adult worm. The smaller number of hooks on the right side of the disc is obviously erroneous. Enlarged 650 times. (According to Beauchamp, 1912).

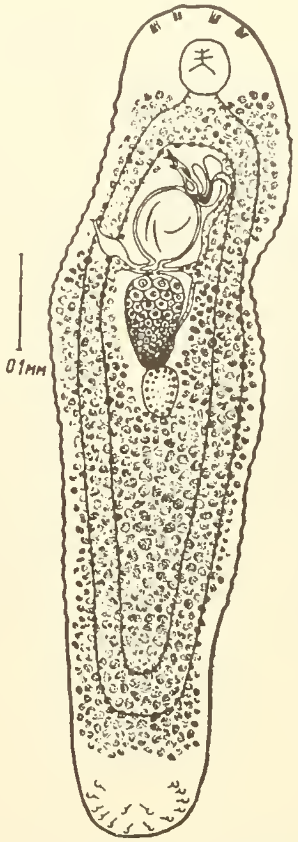

Fig. 44. Acolpenteron nephriticum Gwosdew, adult worm from the gills of Nemachilus stolizkai (Steind.) from the neighborhood of Alma-ata (Kazak, U.S.S.R.)

As stated before, the family Acanthocotylidae possesses a powerfully developed suction-type disc which is provided with numerous chitinous spines articulated with each other and located in radial rows. The number of these rows fluctuates between 20 and 47. Among the genus Lophocotyle there are correspondingly located muscular rays instead of radial rows of spines. Among Enoplocotyle the secondary disc is absent (see page 385).

The true attaching disc of Acanthocotylidae lies on the posterior end of the secondary disc on the ventral side and is equipped with 14 edge and two middle hooks.

Among Microbothriidae (Fig. 49) there is a much-reduced suction-type disc with its interior surface cuticulized to greater or lesser degree. The chitinous armature apparently is completely absent.

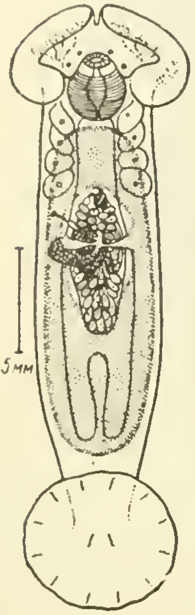

Fig. 45. Anonchohaptor anomalum Mueller, adult worm. (According to Mueller, 1938).

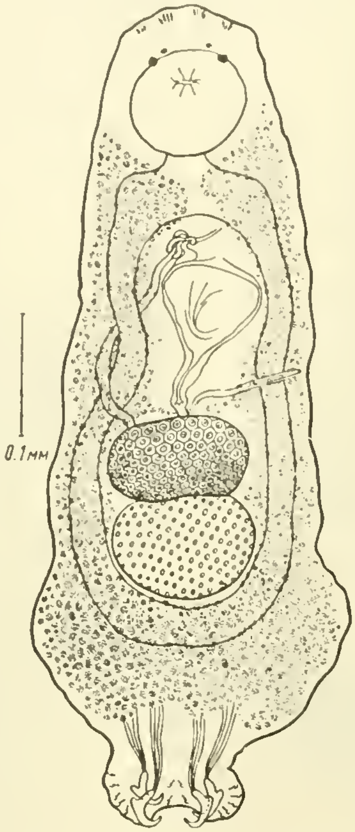

Fig. 46. Protoncyrocephalus strelkowi Bychowsky, adult worm from the gills of Limanda aspera (Pall.) from the region of Yablochnoii (Southern Sakhalin, Sea of Japan).

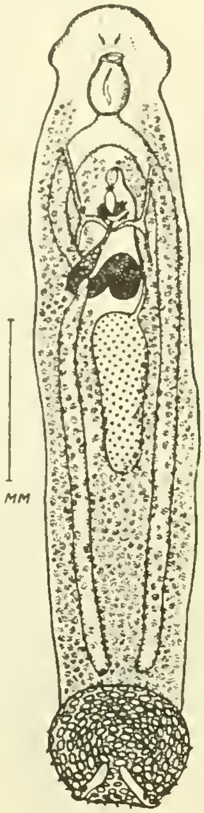

Fig. 47. Catharıotrema selachii (MacCallum), adult worm. (According to Price, 1938).

As regards Polystomatidae, a powerfully developed disc more or less delineated from the body and provided with six suckers, 16 marginal or edge hooks and 2 to 4 middle hooks is characteristic. The latter can be absent (for instance in Neopolystoma, Fig. 15). If they exist, middle hooks are located on the posterior end of the disc, whereas the edge or marginal hooks, numbering six are lying on the anterior edge of the disc, and, further, singly in the center of each sucker, and the remaining four on the posterior edge between the first pair of suckers. p. 37

Sphyranuridae (the only genus Sphyranura, see page 401) is characterized by a disc which is transversely elongated and sharply delineated from the body on which there are two powerful suckers, two middle hooks and 16 edge hooks of which two are located in the suckers and the remaining along the edge of the disc.

Hexabothriidae (Fig. 2) are characterized by the presence of a well-isolated disc, carrying on the posterior end a more or less well-developed appendage of significantly smaller diameter than the disc itself. Six powerfully developed suckers are located on the disc. Along the middle line a strongly curved long hook is located in such a way that its sharp edge is located near the inner surface of the sucker while its remaining portion is located in its interior (or within the tissue of the sucker, nobis). Undoubtedly, in spite of this powerful development these hooks are homologous to the corresponding edge or marginal hooks of the Polystomatidae and other families. The posterior appendage carries two well-developed suckers which are apparently devoid of hooks on its free lower edge. Between these appendage suckers there exists usually one pair of small middle hooks. In a number of species the middle hooks are absent altogether. One must indicate, nevertheless, that the question relative to the chitinous armature of Hexabothriidae demands reinvestigation (see page 406).

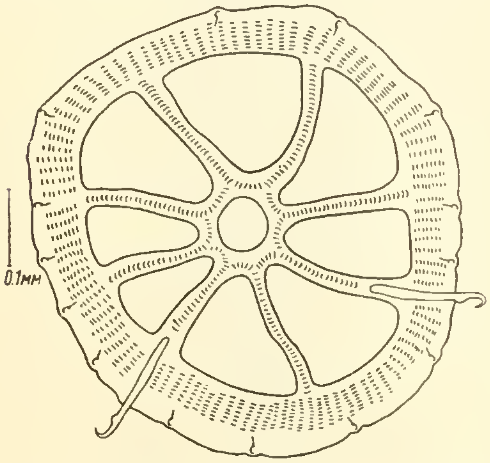

Fig. 48. Heterocotyle sp., attaching disc of an adult individual from the gills of Dasybatus zugei M. H. from the region of Nagasaki (East China Sea).

The family Diclybothriidae close to the preceeding one has an analogous disc, nevertheless six of its suckers, also equipped with powerfully developed chitinous hooks, stand much closer in their structure and function to the valves of the successive families than to the actual suckers. The absence of the chitinous parts characteristic of clamps draws them closer to the latter, but during the research on live subjects it is clearly seen that their common configuration and their method of attachment is of typically valve-type character. The posterior appendage is well developed in the genus Diclybothrium (Fig. 51) and is almost completely reduced in the second genus Paradiclybothrium (Fig. 52). When the posterior appendage is developed, it carries two rudimentary suckers and four pairs of hooks. Two pairs of hooks have the same shape or form as those in the suckers. One pair represents the unchanged small edge hooks and the latter represents small central or middle hooks. (For details see the chapter on embryology, page 101 .) Among Paradiclybothrium the chitinous p. 38

hooks (apparently all four pairs, although so far it has not been possible to detect a pair of the small edge hooks) are preserved together with a strongly reduced appendage, but both suckers (highly reduced to a great extent in the preceeding genus) completely disappear.

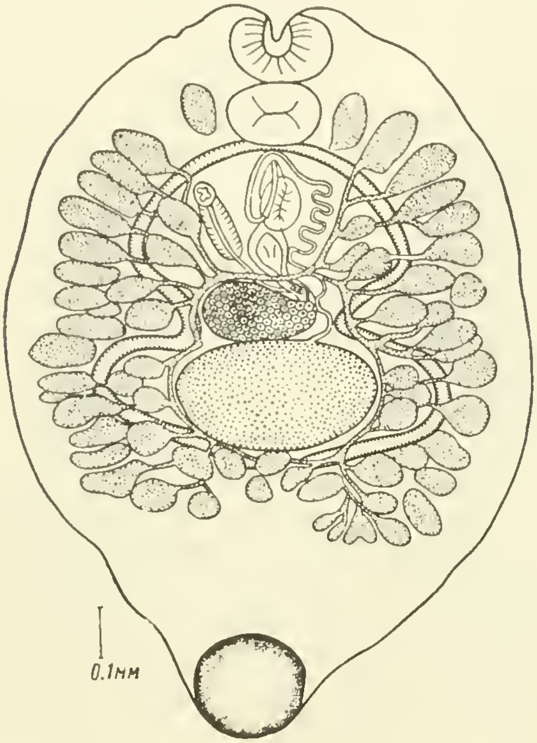

Fig. 49. Leptocotylê minor (Monticelli), adult worm from the skin of the dorsal fin of the young Scyliorhinus canicula (L.) from the Bay of Naples (Mediterranean Sea).

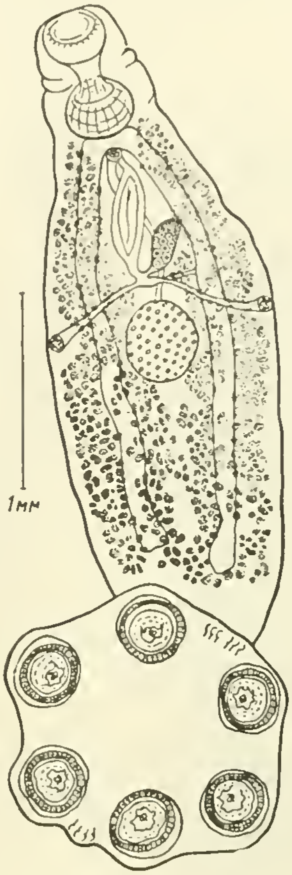

Fig. 50. Neopolystoma palpebrae Strelkow, adult worm from beneath the lower eyelid of Amyda sinensis (Weig.) from Hanka Lake.

The ensuing families (Chimaericolidae, Fig. 53; Mazocraeidae, Fig. 24; Hexostomatidae, Fig. 37; Discocotylidae, Fig. 228; Anthocotylidae, Fig. 42; Plectanocotylidae, Fig. 88; Diclidophoridae, Fig. 54; Microcotylidae, Fig. 23; Gastrocotylidae, Fig. 7; Protomicrocotylidae, Fig. 89) are characterized by the presence of an attaching disc which is delineated from the body of the animal in varying degrees and bears, as a rule, a varying number of chitinous hooks which may be, however, absent in adult forms, and also bearing a varying number of attaching clamps. The number of chitinous hooks fluctuates from one to four pairs and the number of clamps fluctuates from one to several scores (above 100) of pairs. Four pairs of clamps and not more than three pairs of chitinous hooks are charac-

p. 39

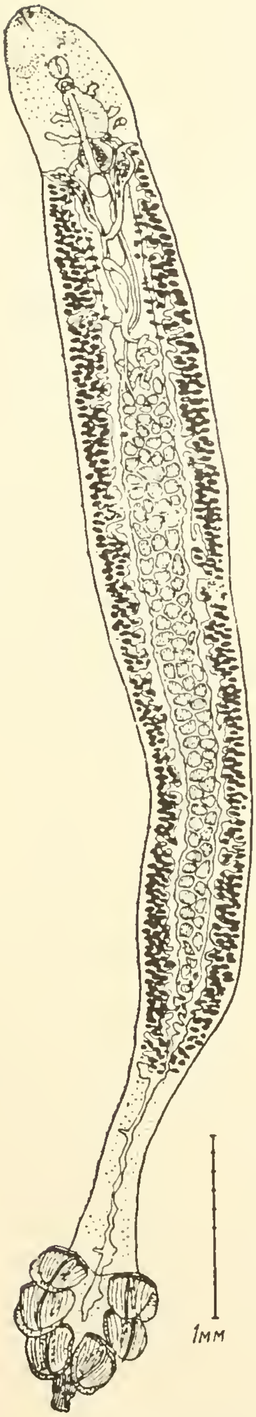

Fig. 51. Diclybothrium armatum Leuckart, adult worm from the gills of Acipenser stellatus (Pall.) from the Delta of the Volga (According to Bychowsky and Gussew, 1950).

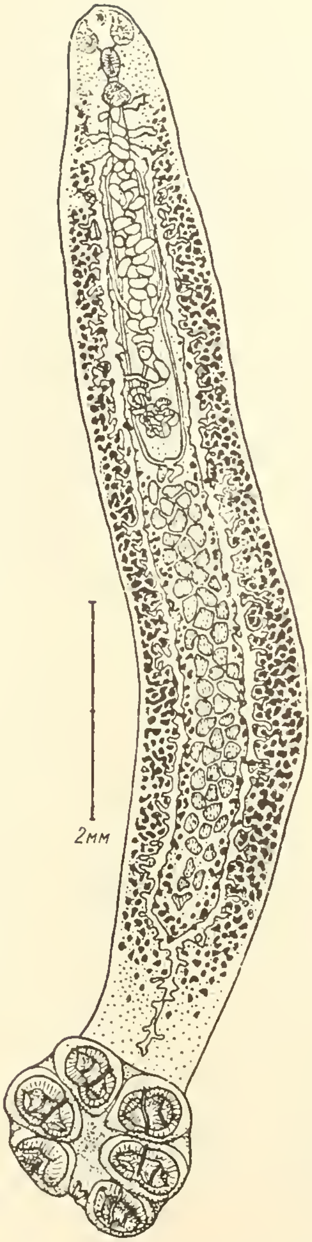

Fig. 52. Paradiclybothrium pacificum Bychowsky and Gussew, adult worm from the gills of Acipenser medirostris Agr. from the Tartar Straits (Sea of Japan). (According to Bychowsky and Gussew, 1950).

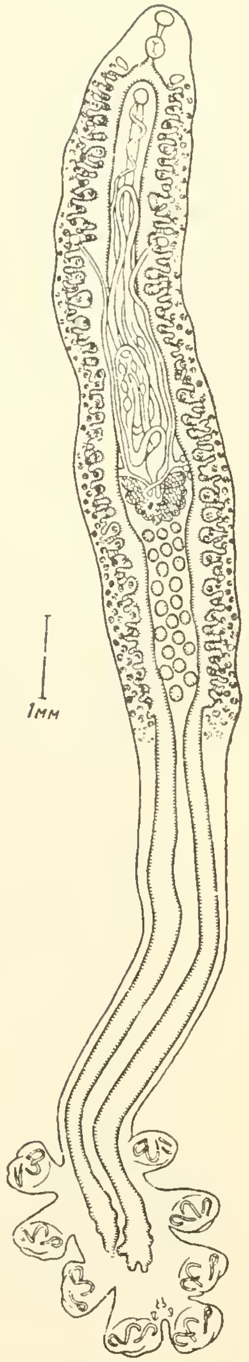

Fig. 53. Chimaericola leptogaster (Leuckart), adult worm from the gills of Chimaera monstrosa L. from the Norwegian Sea near Sere Island.

teristic of the majority of the above-mentioned families,whereas among Gastrocotylidae and Microcotvlidae the number of clamps varies from six pairs upwards, whereas the chitinous hooks, for the most part, number four pairs or are absent in the adult.

External Covers. External covers of monogenetic trematodes p. 40 are represented by a cuticle typical for the parasitic flatworms (Fig. 55), for the most part double-layered, smooth, and comparatively thin, under which is located a more or less well-developed basal membrane which, in a number of cases, is poorly visible. Because of this poor visibility, certain authors question its presence altogether. As a rule, subcuticular cells are absent in the monogenetic trematodes; if in rare cases they exist then they are in relatively small numbers and are under and partially between the fibers of the longitudinal, circular and diagonal muscle layers.

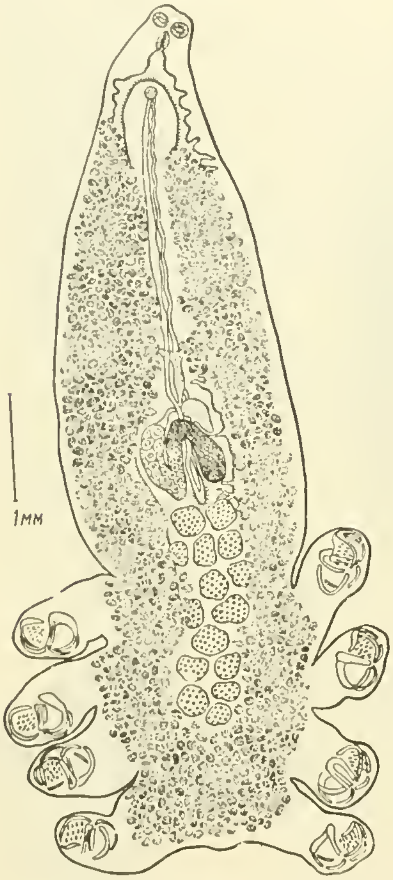

Fig. 54. Dichlidophora denticulata (Olsson), adult worm from the gills of Pollachius virens (L.) from the Barents Sea.

As among other Cercomeromorpha, the question of the covering of the monogenetic trematodes is very complex and there is no commonly accepted opinion concerning its origin. The most widespread is that the cuticle represents a derivative of the ectodermal epithelium which, as a result of its adaptation to parasitism receded into the body and is represented by subcuticular cells or so-called submerged epithelium. This point of view is shared by many zoologists. The comparison of the structure of the coverings in Cercomeromorpha and Turbellaria serves as a basis for this. Thus, in a series of Acoela and Triclada the receding of epithelial cells into the body under the dermal musculature is observed, that is, one observes the relationships which are close to those which are seen among parasitic flatworms. Analogous views can be seen among parasitic Myzostomidae (Fedotov, 1915). However, other points of view exist. Thus, Monticelli, (Monticelli, 1893) supposed that the cuticula represents an ectoderm which underwent complete metamorphosis and which has a changed protoplasm, missing nuclei and missing delineations between the cells. This supposition is based on the finding of circular, round, small bodies in the cuticular structure of the young worms. Finally, a number of researchers headed by Pratt (Pratt, 1909) and Schneider (Schneider, 1873) suppose that adult forms of parasitic flatworms have lost their epithelium completely, which thus is present only among larval stages and is cast off during metamorphosis.

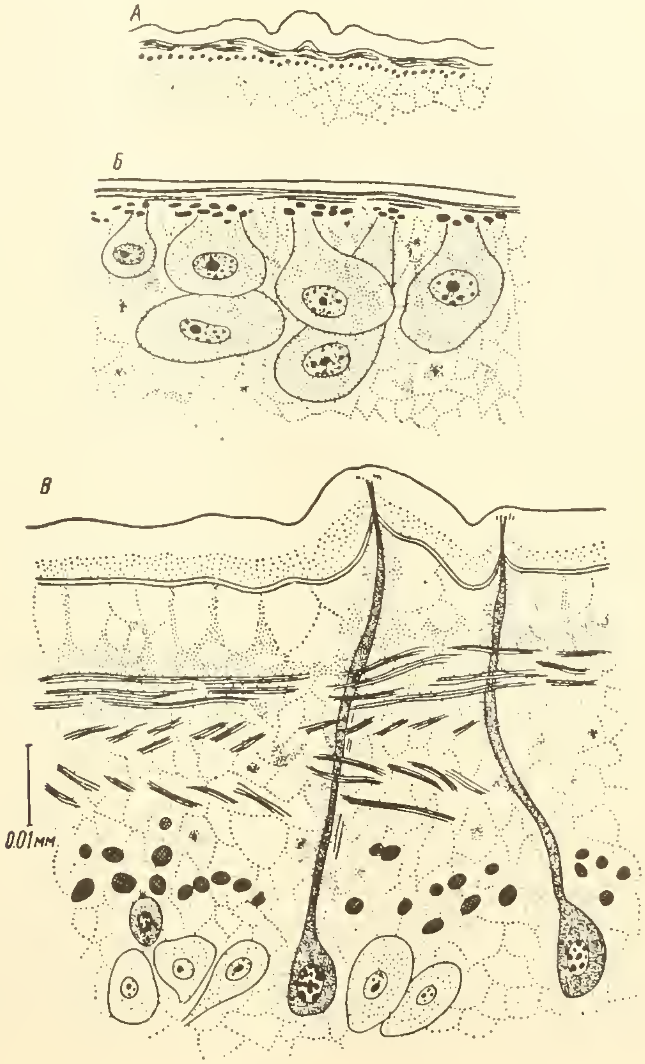

Fig. 55. Coverings of monogenetic trematodes. A--Ancylodiscoides magnus Bychowsky and Nagibina; B--Acanthocotyle williamsi Price; C--Tristoma coccineum Cuvier.

According to this point of view, the cuticle of parasitic flatworms is a derivative of the parenchyma and is equivalent to the basal membrane of Turbellaria. This point of view was advanced in recent times by Poche (Poche, 1929) who proposed to replace the appellation "cuticle" for parasitic flatworms by a new one "pseudodermis" and for subcuticular cells the p. 41
appellation "pseudodermals" (pseudodermal cells).

The opinion of Monticelli hardly corresponds to reality. The remaining two points of view have sufficiently weighty evidence to support them. For monogenetic trematodes we think it more probable that there is no covering epithelium in the adult form, although the first point of view, which is more commonly accepted, deserves more attention. The reasons according to which we are led to the opinion that there is an absence of epithelial cells in the adult forms of monogenetic trematodes are the following. First of all, a majority of authors who studied the coverings of monogenetic trematodes did not discover any traces "of subcuticular cells." p. 42 Thus, during the examination of over 100 species of marine Monogenoidea Goto, Cerfontaine and Maclaren (Maclaren, 1903) never found them once.

Under more careful study, the cells of the receded epithelium of monogenetic trematodes, described by certain authors, appear not to be subcuticular epithelium but various types of glandular cells. Until now, no one has succeeded in presenting convincing views (drawings, nobis) of submerged epithelium among Monogenoidea. The data of I. V. Ivanov (1952) can be considered the only serious material on the subject. Ivanov found, after becoming acquainted with our slides of Acanthocotyle, that among this type, the covers as he writes, "possess all the characteristic peculiarities of the classical submerged epithelium." However, it seems to us that this is not altogether accurate and that at any rate it demands more thorough study. During the study of the same slides one notices that the disposition of the "sub-cuticular" cells, which are clearly seen and which lie in their main aggregate under the dorsal surface of the body of the animal but which can also be seen as well on the ventral side, is not equal.

Basically as is seen from Fig. 55-B, the "little stems" of the cells are not linked to the cuticle but to the muscular fibers located beneath it. In sections one can clearly see that the parenchyma directly joins the cuticle in the spaces between the cut muscular fibers, whereas, one does not observe "the little stems" of the "sub-cuticular cells" in these places. Thus, so far we hesitate to speak with certainty concerning the connection of these cells to the cuticle.

Also, peculiarities of the embryology of monogenetic trematodes seem to us substantial when we see that the ciliated epithelium does not undergo metamorphosis at the attachment of free-swimming larva but peels off completely and falls away. This pertains not only to the species where the ciliated epithelium is arranged in special areas but also to the species where the entire body is more or less covered with ciliated epithelium.

From what has been said above, it is understandable why it seems to us that the most probable supposition is that the cuticle of monogenetic trematodes appears to be a derivative of the parenchyma. The presence of cuticular armature in a number of species can be considered as a substantial objection to this supposition, but at the time of development of the animal, the basic chitinous elements of armament are formed, not directly in the cuticle but in the mass of the parenchyma. How to recognize all these significantly contradictory data without special research does not appear clear to us.[1]

Dermal glandular cells which, as was pointed out, are strongly developed in the main are grouped in the anterior and posterior ends of the body. Near the anterior end they are located mainly along the sides of the pharynx and along the buccal aperture, and open outside terminally or subterminally. Apparently the head glands of Monogenoidea are homologous to the head glands of the larvae of Gyrocotylidae, Cestodaria, Udonellidae, and also to the frontal glands of turbellarians. The glands of the anterior end of the body are most powerfully developed among Dactylogyrus but they are often also encountered among the remaining monogenetic trematodes, and among the latter they are relatively more strongly developed during p. 43 the early stages of the life cycle. The overwhelming majority of the dermal glands are of the sticky or glutinous type and to a lesser degree one also encounters the lachrymous type. The presence of poisonous (narcotic?, nobis) dermal glands, characteristic of a number of turbellaria, is probable among monogenetic trematodes, however, we do not have exact data relative to this subject. Besides the dermal glands there are also glandular cells located in the main body of the parenchyma which are of uncertain origin. These are large cells lying for the most part in groups in the posterior end of the body and opening to the outside in the attaching disc. To this group are related, for example, the powerful cells of the so-called post seminal glands described in detail by Goto and Kikuchi (Goto and Kikuchi, 1917) for Dactylogyrus inversus Goto and Kikuchi, and widely distributed among Dactylogyridae. Excretory ducts of all the dermal glands open on the surface of the body of the animals by unarmed apertures.

Armature of the cuticle occurs relatively rarely. Among Diplectanidae the cuticle is covered by delicate scales predominantly on the posterior half of the body and also partially on the attaching disc (Fig. 56). These little scales have a more or less sharpened front edge which extends freely above the surface, while the more rounded edge lies in the body of the cuticle. Besides that, Rhamnocercinae are armed by real thorns (see page 359). Among a number of Capsalidae there is strong cuticular armament consisting of a varying number of thorns lying mainly along the sides of the dorsal surface of the body. These thorns are located in parallel rows, each consisting of several thorns. The shape of the thorns

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[1] During recent years numerous data concerning the structure of the epithelium of digenetic trematodes and tapeworms were published by Logachev (1953-1955). His works deserve more careful attention.

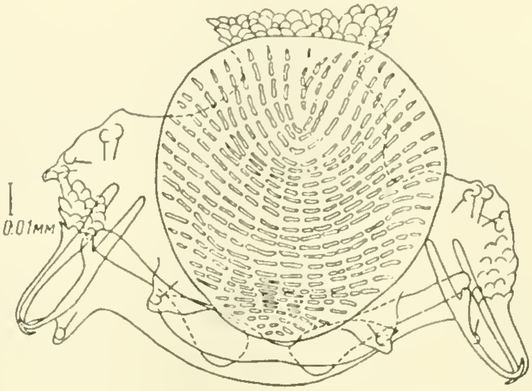

Fig. 56. *Diplectanum aculeatum* Parona and Perugia, the posterior end of the body of an adult worm from the gills of *Corvina nigra* Cuv. and Val. from the region of Karadaga (Black Sea).

varies (Fig. 57) from simply arranged needle-shaped thorns to complex thorns with numerous points on the free edge and with a massive basal part. In a number of cases, these thorns are equipped with special musculature and can move independently of each other. In separate species the number of rows of thorns fluctuates from a significant number (more than 100) to comparatively few (a little more than 10) while among the species with a smaller number of rows the shape of the thorns is usually the most complex. In addition to that, among species with a small number of rows of thorns, the edge of the body forms symmetrical growths, and the thorns are located in the middle of these growths. The complex of the growth with thorns, which is supplied with a special musculature, is very reminiscent of the parapodia of higher worms and undoubtedly represents a primitive formation which aids in locomotion; we called it a propodium (Fig. 58). The question concerning these propodia p. 44 and their development and morphology will be examined in detail in another work. The musculature is very strongly developed among monogenetic trematodes, particularly in the region of the attaching apparatus. It is represented by dermal parenchymatose fibers (concerning the musculature of the sexual ducts and organs, see page 4). The dermal musculature typically consists of circular, diagonal and longitudinal fibers. As a rule the longitudinal musculature is the most powerfully developed, often it forms powerful longitudinal muscular ligatures (ligaments, *nobis*) which are isolated from each other. These ligatures which are mainly located on the posterior end of the body, change into muscles which serve for the movement of the central elements of the attaching armament and for common coordinating movement of the entire attaching disc. According to Maclaren, in *Diplectanum aequans* Wagener (Fig. 59) the longitudinal dermal musculature falls into two layers, exterior--lying directly under the circular layer, and interior--lying under the diagonal layer. Similar relationships have a certain similarity with the disposition of musculature of the dermomuscular sac among Gyrocotyloidea and Cestoidea. There are indications which point to the absence of the diagonal musculature among certain Hexabothriidae.

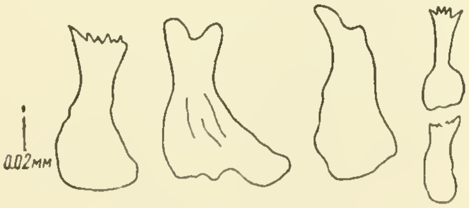

Fig. 57. Skin thorns of various shapes, Capsalidae.

It is curious that among certain forms (for instance Diclybothriidae) one observes more powerful development of the dorsal musculature, whereas among the majority of monogenetic trematodes the musculature of the ventral side is the most powerfully developed. Parenchymatose muscular fibers are chiefly located in the main portion of the body in more or less well-developed dorsoventral bunches. Less frequently, one encounters fibers which stretch longitudinally as in Cestoidea. Such disposition of the fibers is usually observed in the anterior or posterior ends of the body.

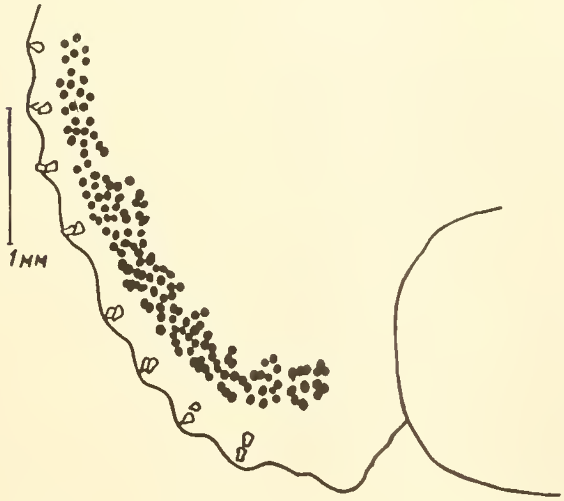

Fig. 58. Capsaloides sp., propodia of the adult worm from Tetrapturus sp. from the region of Woods Hole (Atlantic Ocean).

Parenchyma. Parenchyma fills the entire body between the dermal muscular sac and the internal organs and has the appearance of polygonal cells, or more seldom syncytial tissues with numerous interior gaps between the cells which are filled with a colorless fluid. The latter is devoid of formed elements. Often parenchyma has a fibrillar p. 45 structure; sometimes it is differentiated, it is true to a small degree, into ecto- and endoparenchyma as occurs in Cestoidea. As Goto indicates, parenchyma divides very sharply into ectoparenchyma and endoparenchyma in Heteraxine heterocerca Goto. At the same time, he even notes the presence of a special membrane which lies between these layers (Fig. 60).

Digestive System. The digestive system for the most part is very strongly developed among monogenetic trematodes. It is represented by a pharyngeal apparatus, esophagus and intestine.

The buccal aperture is located subterminally and less often terminally. Around the buccal aperture one can sometimes observe lip-like growths, more often, however, its edge is smooth. The buccal aperture usually leads into the buccal funnel which is often surrounded by a more or less isolated sucker, or on the interior edges of the funnel there can be, as has been mentioned above, two suckers developed in varying degrees. All these formations serve for the attachment of the anterior end of the worm's body during feeding. Posterior to the buccal funnel lies a more or less well-developed buccal

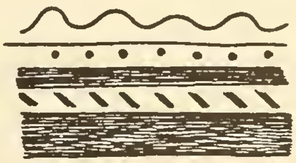

Fig. 59. Diplectanum aequans Wagener, diagram of the cross section of the ventral coverings. (According to Maclaren 1903)

cavity which changes into a sac close to the pharynx or prepharynx.

This prepharyngeal sac has the same structure as in Rhabdocoela. Among a number of species the pharynx can protrude to the outside (the majority of the lower Monogenoidea), but among others it is devoid of this capability.

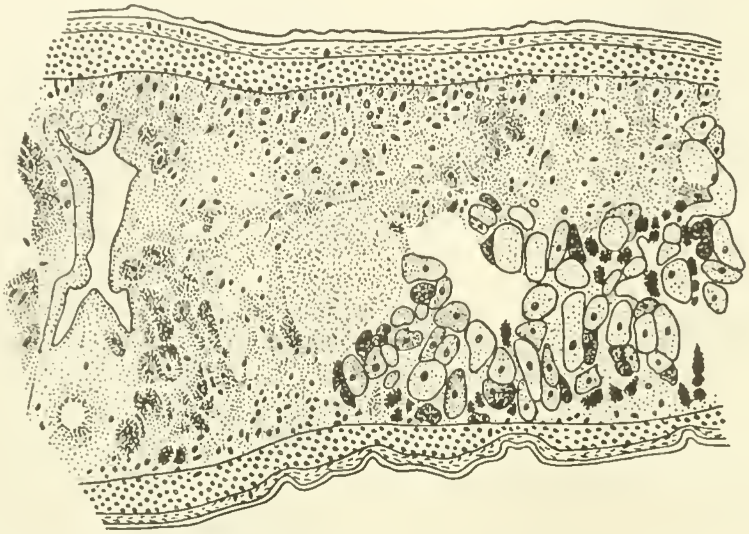

Fig. 60. Heteraxine heterocerca (Goto), cross section of the body below the sex aperture. Enlarged 200 times. (According to Goto, 1894).

Pharynx. The pharynx is usually the very powerful type of pharynx plicatus and pharynx bulbosus of the Turbellaria. Its form is round and somewhat elongated, in rare cases barrel-shaped, egg-shaped, etc. The pharynx is separated from the sac or parenchyma which surrounds it by a special membrane; this same type of membrane limits its interior lumen which often has a tetrahedral outline. The structure of the pharynx is complex and to a known degree resembles the structure of the suckers which can also be explained by a functional similarity (among certain Capsalidae the pharynx even functions in place of the anterior suckers). p. 46 Usually in the pharynx there is a strongly developed musculature which consists for the most part of three layers, external and internal circular layers and the middle radial layer (Fig. 61). Very often there are weakly developed longitudinal fibers. Often the number of the layers increases and the pharynx becomes much more complex. Between the muscular fibers are located the numerous nuclei belonging to the muscle cells and often mononuclear pharyngeal glands are located in the main part of the pharynx. The latter can lie also in the adjacent parenchyma and only pierce the body of the pharynx by their canals. Very often very powerfully developed supplementary glands called salivary or postpharyngeal open into the lower end of the pharynx along with these glands (Fig. 62). Among certain Gyrodactylidae the pharynx is divided into two parts of which the first consists of several pyramidal cells and the posterior part is rounded, usually of muscular structure (Fig. 63).

The pyramidal cells of the interior part of the pharynx of the Gyrodactylidae possess great mobility and can powerfully extend and contract. Their function is not known, but apparently they have a certain relationship to the pulling off of the epithelial cells of the host during feeding.

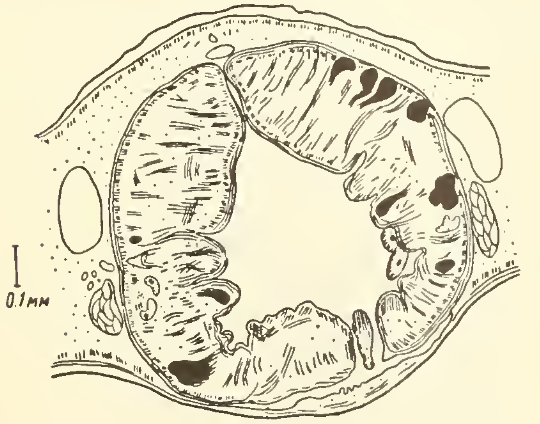

Fig. 61. Nitzchia sturionis (Abildgaard), cross section through the pharynx of the worm, from the buccal cavity of Huso huso (L.) near the Island of Sara (Caspian Sea).

Among monogenetic trematodes the esophagus for the most part is short or may be completely absent. Among forms with relatively long esophagi it often forms lateral blind outgrowths which can branch strongly. In other cases, the esophagus has the appearance of a straight pipe and changes directly into the intestinal tract. Among many forms, the presence of a powerful muscular sphincter, the contraction of which interrupts the passage of food into and out of the tract at the beginning of the esophagus, is characteristic. Numerous monocellular glands, which are observed in certain Monocotylidae, can open into the esophagus. It is interesting that these glands are absent among the highest monogenetic trematodes, for instance among Microcotylidae and Hexabothriidae. Goto also calls these glands "salivary."

Intestine. The intestine of monogenetic trematodes historically p. 47
evolved from the sac-like one of Rhabdocoela and during the individual ontogeny also undergoes a similar stage (see the chapter on embryology) and is characterized by the absence of an anal opening. Usually the intestine has the appearance of two trunks stretching along the entire body, less often it is simple in the form of a more or less long pipe (Tetraonchidae, Figs. 29, 64; Tetraonchoididae, Figs. 29; and certain others). The two-branched intestine can be of varied shape. Intestinal trunks can be smooth in the shape of cylindrical pipes and end blindly (Gyrodactylidae, Fig. 12, a number of Ancyrocephalinae etc.), or they can have a number of lateral growths and branches along their length and finally,

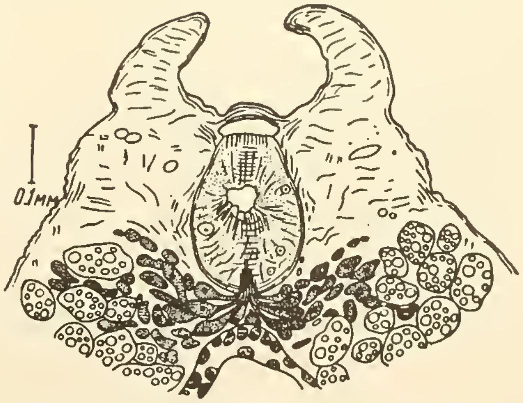

Fig. 62. Polystoma integerrimum Froelich, frontal section of the anterior part of the body. Salivary glands appear dark.

forming or not forming any branches, they may merge at the posterior end of the body, forming in this fashion a round or ellipsoidal figure (Dactylogyridae, Fig. 5). Very often when the ends of the intestinal trunks merge, a single smooth or branched extension stretches from the place of the junction posterior towards the attaching disc. The formation of lateral branches is observed both in forms with the two-trunked intestine as well as among the single-trunked, as for instance in *Diplozoon paradoxum* Nordmann(Fig. 231). We also note that the growths and branches of the intestinal trunks oriented inside the body can merge forming anastomoses between two trunks and giving the intestines a strongly-branched form (*Polystoma*, Fig. 22). Often the development of p. 48
these anastomoses is so powerful that the basic trunks become indistinguishable (for instance among certain Microcotylidae, Fig. 66). Basically, smaller worms have a simpler form of intestine. The latter reaches the greatest complexity among the larger marine forms. One must note that complication of the intestine is observed independently in various systematic groups and is correlated with an increase in the size of the animal. Undoubtedly, a more equitable distribution of the food substances which are

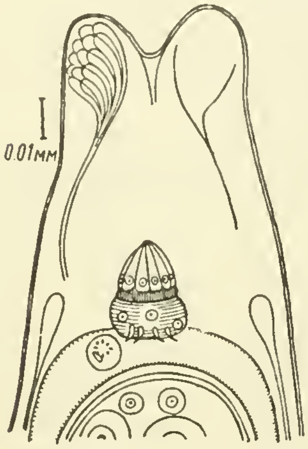

Fig. 63. *Gyrodactylus atherinae* Bychowsky, anterior end of the body of an adult worm from the gills of *Atherina mochan pontica caspia* Eichw. near the Island of Sara (Caspian Sea). Strongly flattened (semi-diagrammatic).

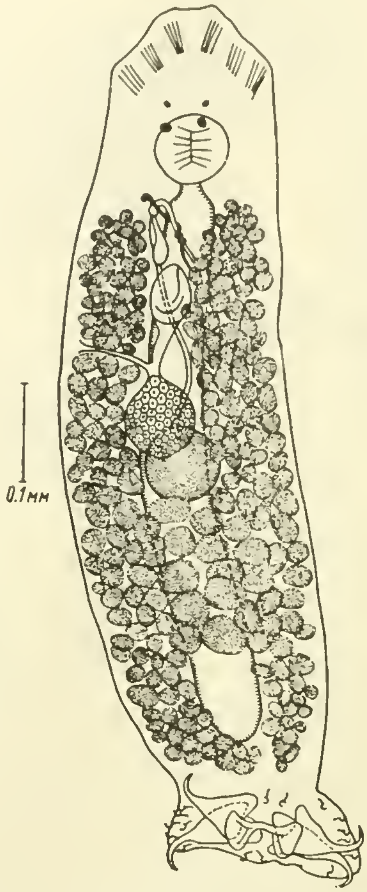

Fig. 64. *Tetraonchus monenteron* (Wagener), adult worm from the gills of *Esox lucius* L. from the Delta of the Volga. Vitelline follicles at the posterior end of the body are somewhat rarified.

absorbed by the walls of the intestine among the parts of the body of the animal is attained by this means. The structure of the intestinal wall, as the researches of Goto show, can be of two types. The first type is characteristic of Microcotylidae, Mazocraeidae, Diclidophoridae, and Hexabothriidae, and is distinguished by the fact that there is no continuous epithelium in the intestinal wall but instead isolated large epithelial cells with numerous pigmented granules are situated upon the tunica propria (Fig. 67). The second type peculiar, according to Goto, to Gyrodactylidae p. 49 Dactylogyridae, Monocotylidae and Capsalidae, is represented more or less by a typical cuboidal or columnar epithelium sometimes arranged in several layers (Fig. 68). For the forms of the first type, the absence of salivary glands of the esophagus is characteristic; for the second, their presence. Apparently, both types of digestive tracts are linked with different means of digestion. For the first type, digestion probably occurs inside the intestinal canal, in the second type--intracellular, by way of active seizure of food particles which are prepared by the "salivary" glands. The picture of the intracellular digestion can be well observed in a number of forms, particularly among Polystomum integerrimum Froelich (Fig. 69). As a matter of fact, this question demands further special investigation.

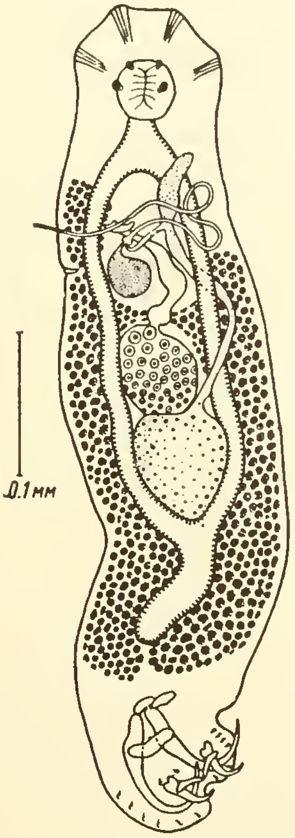

Fig. 65. Anclyodiscoides siluri (Zandt), adult worm from the gills of Silurus glanis L. from the Delta of the Volga.

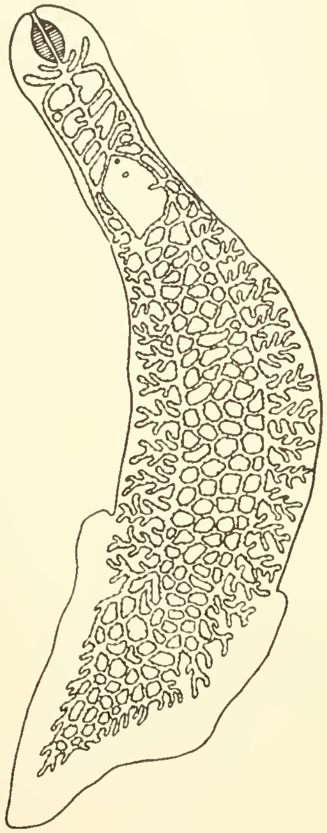

Fig. 66. Microcotyle reticulata Goto, adult worm. Natural size 6-10 mm (According to Goto, 1894).

Excretory System. The excretory system has been studied comparatively poorly. As opposed to the system of digenetic trematodes, among Monogenoidea it apparently does not have systematic significance. In essence, the excretory system is composed of three parts: Protonephridia and their capillaries and system of ducts including basic trunks and end parts, which connect the excretory system with the outside. The protonephridia of monogenetic trematodes are in the shape of the usual end cells with ciliary flame. The capillaries leading from them resemble thin-walled pipes, often bearing on their walls ciliated epithelium as among the Turbellaria. Apparently these capillaries are intracellular formations. The number and disposition of these flame cells have been studied very insufficiently. The number of terminal protonephridial cells varies among the adult forms (among the young ones see chapter on embryology). Thus in the anterior end of *Diplectanum* the number of flame cells, according to our observations, is not less than six on each side (Fig. 70). The capillaries of protonephridia empty into canals which successively increase in size and merge together to form two main ones which are loacted along the sides of the body. The main canals stretch from the anterior end to the posterior end and sometimes reach into the attaching disc and return to the anterior end, often intertwining with its first half. The relationships between both halves can be very complex. Among the majority of Dactylogyridae, Monocotylidae, Capsalidae, and Polystomatidae and basal trunks p. 50
in the anterior part of the body at the level of and somewhat higher than the pharynx form a rather complicated wavy part and join by cross commissures so that its excretory system is no longer separated into right and left independent parts but becomes unified (Fig. 71). Apparently among a number of forms there are similar connections also at the posterior end of the body, as for instance in *Monocotyle ijimae* Goto (Fig. 72). Among *Calceostomella inermis*, Parona and Perugia, basic ducts are faintly noticeable because

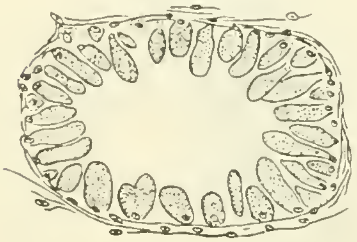

Fig. 67. *Squalonchocotyle spinacis* (Goto), cross section through the intestinal branch. Enlarged 204 times. (According to Goto, 1894).

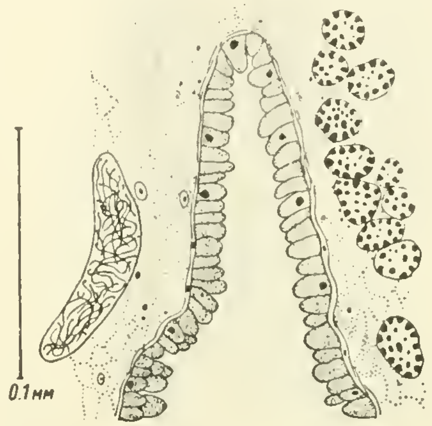

Fig. 68. *Nitzschia sturionis* (Abildgaard), cross section through the intestinal branch. Worm from the gills of *Huso huso* (L.).

the entire excretory apparatus acquires a netlike character where a large part of the small as well as the large canals are equipped with a powerfully developed ciliated cover. Among a majority of forms the excretory system is colorless but among representatives of the genus Calceostoma the walls of the vessels and their liquid contents are often darkly tinted.

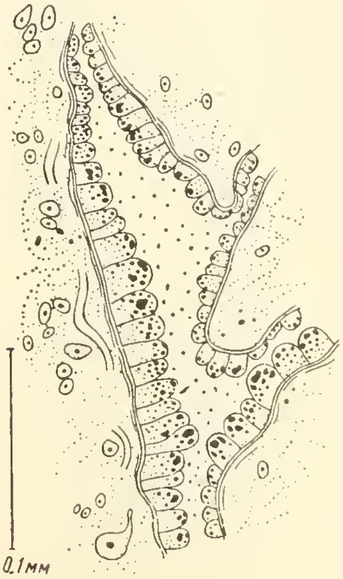

Fig. 69. Polystoma integerrimum Froelich, sagittal section through the intestinal branch. The remnants of the frog's red blood corpuscles in the process of being digested appear in black in the cells of the intestinal epithelium.

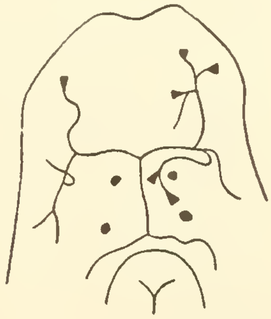

Fig. 70. Diplectanum aculeatum Parona and Perugia, excretory system of the anterior end of the body of an adult worm from the gills of Corvina nigra Cuv. and Val. from the region Karadaga (Black Sea). (Semi-diagrammatically).

The terminal parts of the excretory system are located at the level of the pharynx or somewhat lower. They consist, on each side of the body, of a single canal which often forms, at some place along its length, a more or less well-developed contractile bladder--excretory bladder equipped with special musculature. The excretory vesicles or bladders open to the outside by independent apertures which are located either laterally or more often dorsolaterally. The small duct which is usually present between the excretory aperture and the bladder is equipped with a powerful muscular sphincter. Excretory vesicles are well-developed among many monogenetic trematodes but weakly noticeable among Mazocraeidae, Microcotylidae, and families related to them.

Nervous System. The nervous system is relatively strongly developed and in some respects it is simplified in comparison with the turbellaria and in other respects it is significantly more complicated. The p. 51
cephalic brain among more primitive forms is located dorsally in front of the pharynx (Dactylogyridae, Tetraonchidae and others), and among more highly developed types, above the pharynx itself (Polystomatidae) or directly posterior to it (Microcotylidae and others). For the most part, the brain consists of two powerful ganglia joined by a single dorsal commissure (Figs. 73, 74). Among certain forms, head ganglia are joined by means of the dorsal and ventral commissures thus forming a nerve ring around the esophagus (Capsala, Nitzschia and others). Three to four pairs of anterior nerves emerge from the head ganglia, sometimes immediately separating into individual fibrillae and innervating the anterior end of the worm. As a rule, three pairs of nerve trunks emerge behind the head ganglia: dorsal, lateral, and ventral. As a rule, the ventral pair is the most powerful and often forms a special ring of attaching disc on which are sometimes located the gangliose widenings corresponding to the attaching organs. Among the forms with asymmetrical attaching apparatuses, the ventral nerve trunks are also usually asymmetrical (Fig. 75). Among a number of forms the dorsal pair of nerve trunks is weakly developed and among some of them is

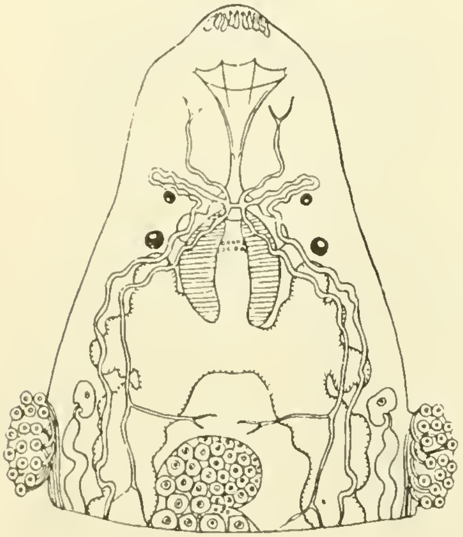

Fig. 71. Polystoma integerrimum Froelich, head end of an adult worm showing the excretory system (junction of the right and left halves of the ducts in the anterior part of the body). (According to Zeller, 1872, simplified).

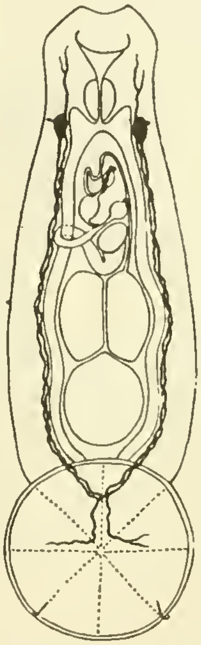

Fig. 72. Monocotyle ijimae Goto, structure of the excretory system (the junction of the right and left halves of the ducts ! in the posterior part of the body). (According to Goto, 1894).

completely absent (as for instance among certain Diclidophoridae). The lateral pair of nerves always exists but is usually thinner and shorter than the ventral. Between the trunks commissures can be seen as was noted by Lang (Lang, 1880) for *Capsala martinieri* Bosc (=*Tristomum molae*, *auct*.) (Fig. 76). The nerves which lead from the main nerve trunks p. 52
usually divide into a network of nerves which interlace the entire periphery of the animal. When the nervous system of monogenetic trematodes and Rhabdocoela are compared, a complete coincidence of main traits is evident (aside from the secondary traits which are connected with the powerful development of the attaching organs among monogenetic trematodes).

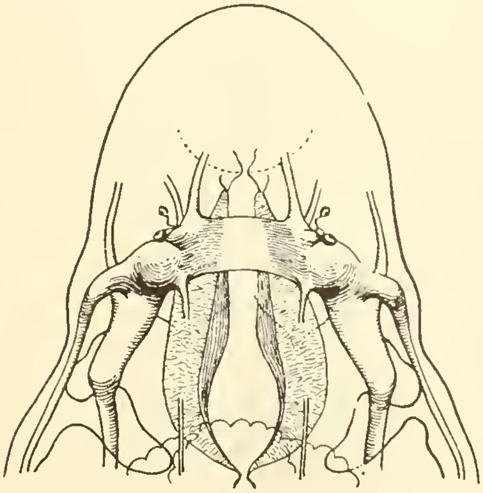

Fig. 73. *Polystoma integerrimum* Froelich, diagram of the anterior part of the nervous system of an adult worm, dorsal view. (According to Andre, 1910).

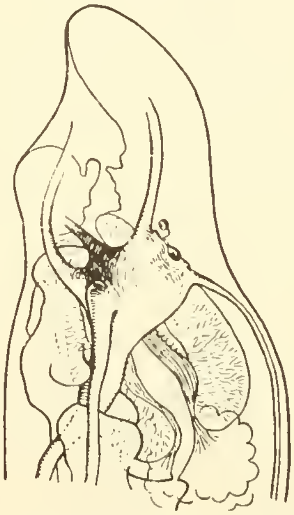

Fig. 74. *Polystoma integerrimum* Froelich, the same diagram, lateral view. (According to Andre, 1910).

Especially interesting are two aspects--immediate separation of the anterior nerves into separate fibrillae, and the weak development of the commissures between the main nerve trunks within the limits of both groups.

Organs of feeling are represented by eyes and sensitive nerve endings scattered within the cuticle along the entire body, but which occur in greater numbers close to the anterior edge and near the attaching organs. The sensitive fibrillae described by a number of authors apparently do not exist.

It has not yet been ascertained if the special suckers located on the dorsal side of a number of Capsalidae have any relation to the organs of feeling.

The eyes of monogenetic trematodes are mostly paired in two pairs or more seldom, one pair. Among the highest Monogenoidea one finds only one eye but of the paired type by its origin. The indication of the presence of six to eight eye spots in (*Hexabothrium appendiculatum* Kuehn) was erroneous as we have explained before. What was mistaken for eyes proved to be glandular cells. The eyes are located on the dorsal side of the body usually above the pharynx or in front of it closer to the anterior end. For the most part, eyes are of different sizes--the anterior pair is usually smaller than the posterior, however, the reverse relationship is also observed. Often the eyes are strongly reduced or even completely disappear. The reduction and degeneration of the eyes can be easily traced in a number of Dactylogyridae especially among representatives of the genus *Acolpenteron* which are parasites of the ureters of their hosts. p. 53
A number of forms have eyes only in the early stages of development. The structure of the eyes is primitive enough (Fig. 77). Usually the eye is inverted and consists of a pigmented globule in the shape of one large cell varying in color from amber to black and consisting mostly of unicellular retinae with a fringe of rods adjoining directly the pigmented globule from its concave side or adjoining a special layer lying between the retinae and the pigmented globule. These rods are usually analogous to the eye rods of higher animals. Among a number of forms there is also a special light refracting little-lens which lies in front of the eye globule. Andre's

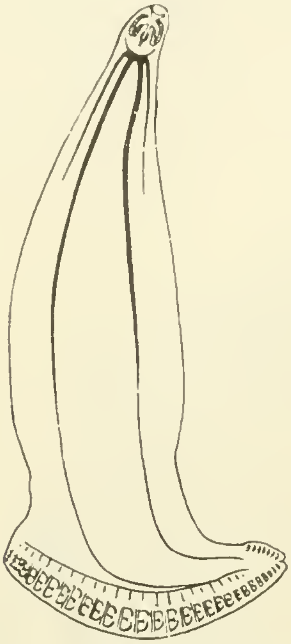

Fig. 75. *Heteraxine heterocerca* (Goto), nervous system of the adult worm. (According to Goto, 1894, simplified).

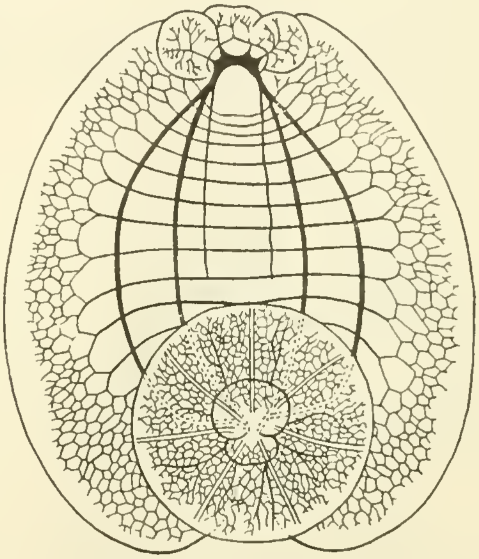

Fig. 76. *Capsala martinieri* Bosc, nervous system of the adult worm. Somewhat diagrammatized and and simplified. (According to Lang, 1880).

assertion (Andre, 1910b) of the absence of these lenses among Polystoma integerrimum Froelich is erroneous and is based on a study of small numbers of young individuals; the presence of lenses in a number of monogenetic trematodes was verified by us not only on live subjects but also on slides stained with the usual histological colors. Among forms having a single eye, the eye is usually equipped with two lenses which enables us, during the study of live subjects, to suggest that such an eye is a result of the fusion or merging of the two eyes first existing in phylogenesis. Eye-nerves are usually very short and emerge from the dorsal side of the anterior part of the head ganglia. As Goto accurately points out, among adult monogenetic trematodes the eyes are in the process of disappearing and apparently do not function.

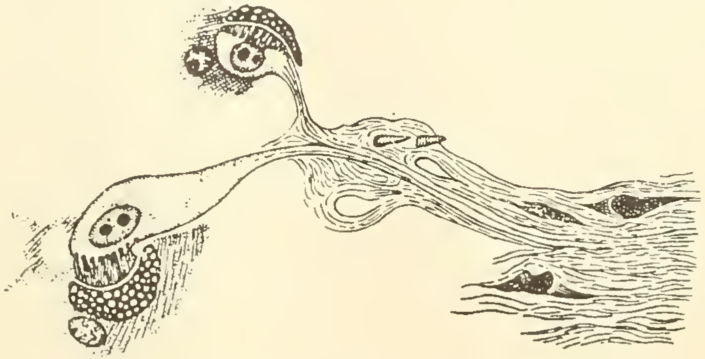

Fig. 77. Polystoma integerrimum Forelich, two eyes from one side of the body, semi-diagrammatic. Enlarged about 1300 times (According to Andre, 1910).

From all of our observations, it is clear that the growth of the eyes occurs only during the time of the development of larvae in the egg; once it emerges from the egg its eyes grow no more and in many forms the p. 54 eyes are subjected to reduction or even complete disappearance during ontogenesis.

Sex System. All monogenetic trematodes without exception are hermaphrodites. They usually have one common sex pore (porus genitalis communis), leading into the sex atrium into which opens the seminal ejaculatory canal or the male copulative organ and finally the uterus; rarely there are separate openings of the male and female sex systems; sometimes the seminal ejaculatory duct opens into the terminal part of the uterus. Usually the common sex opening is located more or less medially on the ventral side of the body, posterior to the esophagus or posterior to the bifurcation of the intestinal trunk; more rarely it is located slightly to the side in front of or behind the intestinal trunks, or it can be displaced completely laterally. In addition to the common sex pore, among a majority of forms there exist one to two vaginal openings which are located in different positions either on the ventral side or along the sides, or on the dorsal side of the body and may be located both at the level of the ovary and closer to the anterior end or, on the contrary, to the posterior end of the body. Thus, among monogenetic trematodes the number of external pores of the sex system fluctuates from one to four. In addition to that, among many forms, predominantly the more highly organized ones, there is a special duct of the sex system which connects it to the digestive system (see page 71).

The sex atrium, (*atrium genitale communae*) (Fig. 78) is present among a number of monogenetic trematodes and in the simplest cases represents a small cavity separated from the external medium by a narrow part and resulting from a drawing-in of the exterior cuticle and often equipped with special musculature. Into this sex atrium the uterus opens more ventrally, and the male sex system also opens somewhat closer to the dorsal surface. Along with such simple structure of the atrium considerable complications occur. Often the common atrium forms two more or less well-developed concavities into which sex ducts open. The common

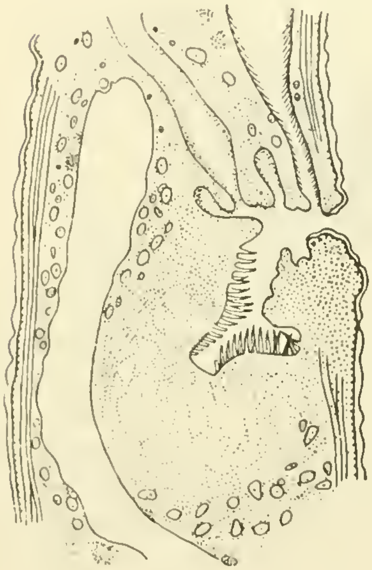

Fig. 78. *Microcotyle sebastis* Goto, sagittal section through the body of the worm in the region of the sex atrium. Enlarged 245 times (According to Goto, 1894).

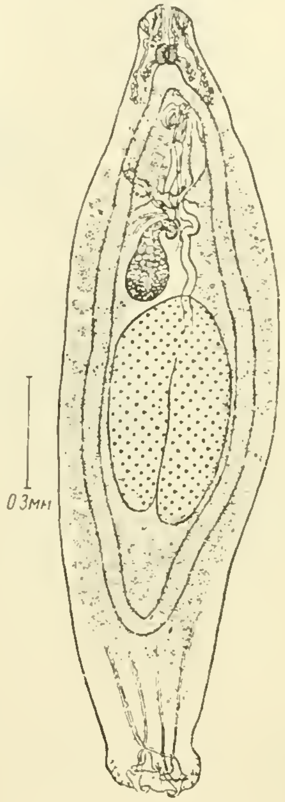

Fig. 79. *Parancyrocephalus daicoci* Yamaguti, adult worm. (According to Yamaguti, 1938).

cavity can remain sufficiently large or be considerably reduced in size.
These concavities, which were formed in a secondary fashion, can be con-
sidered as male or female atria (*atrium masculinum* and *atrium feminium*).
Independently from the isolation of the divided atria, a chitinous armature
in the shape of varying forms of hooks analogous and perhaps even homol-
ogous to those of the male copulatory apparatus is formed on the upper in-
terior surface of the common sex atrium among many more highly organized p. 55
types, especially among Microcotylidae. These hooks, which are charac-
teristic for the separate species, can be located directly on the upper wall
of the atrium or in the special concavity or even in a special muscular sex
papilla separated by a special membrane from the surrounding tissues but
not connected with the terminal part of the male sex ducts.

The male sex system among monogenetic trematodes is represented by well-developed seminal ducts, seminal reservoirs, supplementary glands, and a copulatory apparatus.

The male gonads for the most part are in the shape of rounded
bodies, more rarely they are lobulated or of some other form. The
number of testes varies but the basic number is one. The opinion of Fuhr-
mann that the two testes appear to be primary is completely faulty and is
based on an analogy with digenetic trematodes. Within limits of the sepa-
rate groups the number of testes is smaller among the most primitive forms
than among the highly organized ones. Thus among *Dactylogyrus* and, close
to it, *Ancyrocephalus* and others, the number of testes always equals one.
In the species *Parancyrocephaloides daicoci* Yamaguti, a form which is
close to the ones mentioned above, there is also one testis but it is bifur-
cated from the posterior end almost to the anterior edge (Fig. 79). The p. 56
fact that we deal here with the beginning of the bifurcation of the testis and
not with the reverse process is substantiated by the presence of a single
seminal duct emanating from the anterior end of the testis. Finally, among
the more highly organized form *Linguadactyla molvae* Brinkmann, related
to the same group, the number of gonads is considerable (Fig. 21). With-
in the limits of the aberrent group, Microbothriidae, there is one testis
among *Leptobothrium* and *Leptocotyle*, there are two lying symmetrically
side by side among *Dermophthirius* and finally, many in the shape of
follicles closely pressed to each other among *Microbothrium*. Among Mono-
cotylidae there is a number of genera having from one to a multitude of
testes. Among representatives of *Heterocotyle* and *Dasybatotrema* there
is only one testis (Fig. 80). *Empruthotrema raiae* MacCallum has a testis
bifurcated from the anterior end almost to the posterior end or, to be more
precise, folded in two because the seminal duct emerges from one of the
anterior ends (Fig. 15). Among the species of the genus *Dionchus* there
are two testes lying one behind the other (Fig. 16), and among *Monocotyle*--
three, of which one lies behind and two symmetrically side by side and p. 57
closely contiguous in front of the rear one (Fig. 27). Finally among many
genera, as for instance *Calicotyle* there are numerous testes (Fig. 81).

Among Polystomatidae the increase in the number of testes from one (genus Polystomoides and others, Fig. 82) through two (Diplorchis, Fig. 83) to 25 and more (Sphyranura, Fig. 35) is distinctly visible. The greatest number of testes occurs in Microcotylidae where it can be in excess of 200 among separate representatives. However, in the odd genus Mazocraeoides there is only one testis (Fig. 84). The process of increase of the number of testes undoubtedly takes place independently in the different groups. In the majority of cases this increase is realized by the way of resulting division of the primary testis, mainly in a transverse direction to the testis and only after that in a longitudinal direction. Thus, this process takes place in all elongated forms. The increase of the number of testes from the beginning by the longitudinal subdivision occurs more rarely, mainly among types with considerable width.

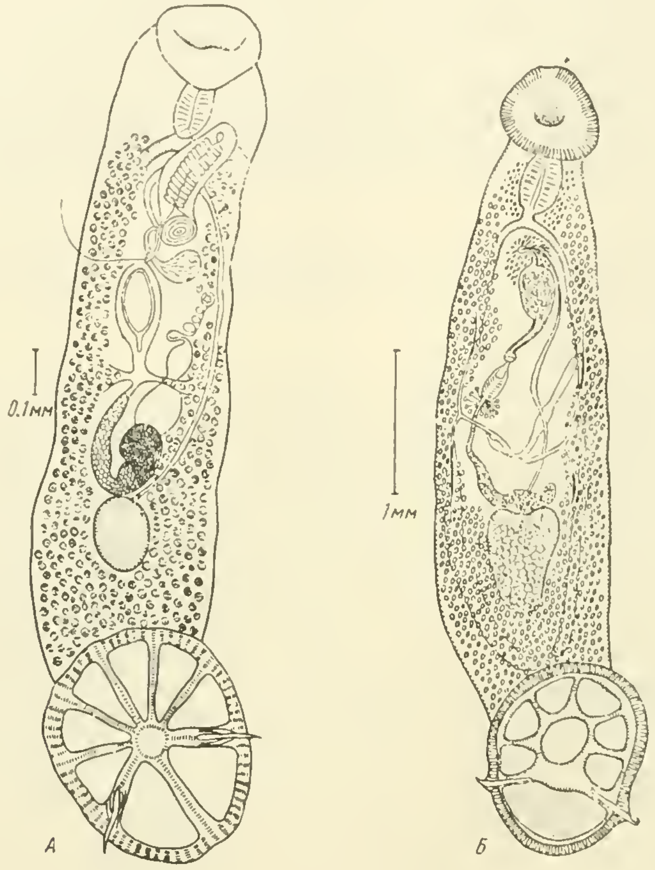

Fig. 80. A--Heterocotyle sp., adult worm from the gills of Dasybatus zugei M.H. from the region of Nagasaki (East China Sea), (original); B--Dasybatotrema dasybatis (MacCallum), adult worm. (According to Price, 1938).

In certain cases the testes represent a follicular mass located closer to the ventral side of the body, a mass about which it is difficult to say whether it represents a single or multiple organ (Fig. 85). Among the

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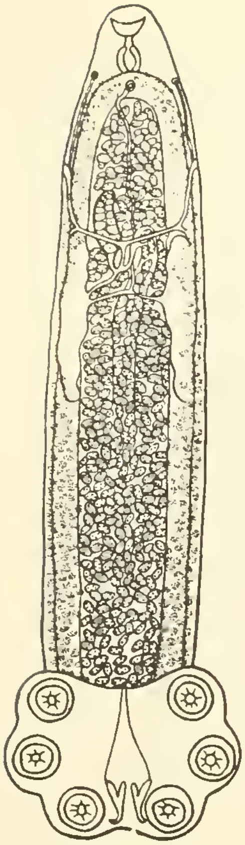

Fig. 83. Diplorchis ranae Ozaki adult worm. Enlarged 16 times. (According to Ozaki, 1935).

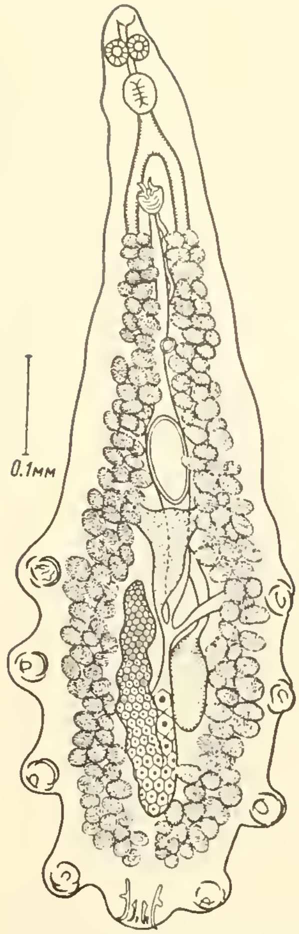

Fig. 84. Mazocraeoides dorosomatis Yamaguti), adult worm from the gills of Clupandon punctatus Sohl. from the region of Kagoshima (East China Sea).

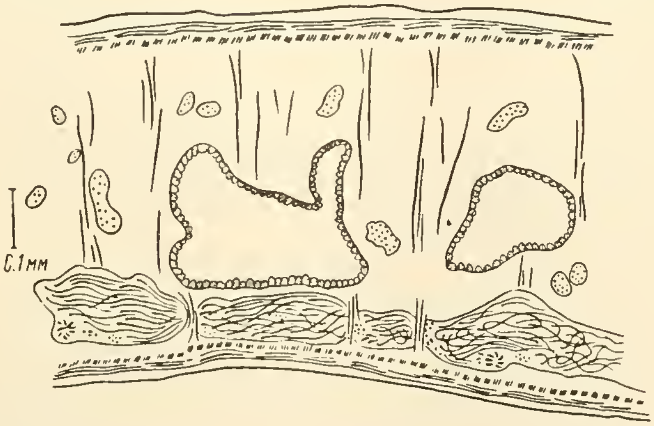

Fig. 85. Polystoma integerrimum Froelich, sagittal section through the body in the region of the testes.

well-known Polystoma integerrimum Froelich the transition from a single rounded testis to such a follicularly-merged one takes place during the ontogeny by way of the considerable growth and individualization of separate parts. p. 59

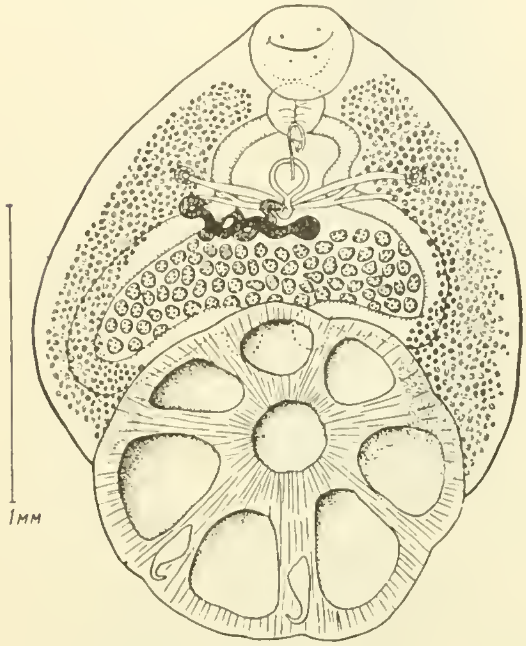

Fig. 81. Calicotyle kroyeri Diesing, adult worm from the skin near the anal opening of Raja batis L. near the southern shores of England (Atlantic Ocean). Four eyes are visible on the buccal sucker.

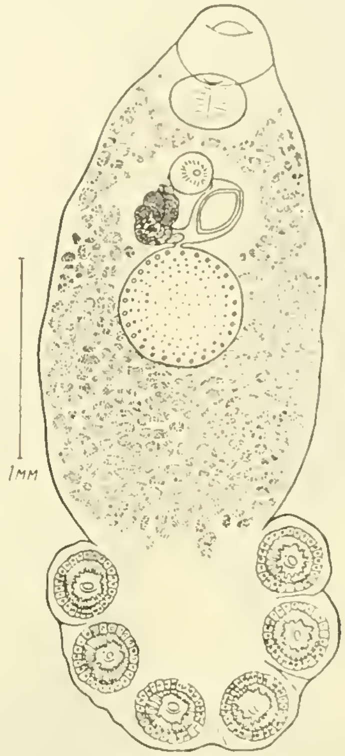

Fig. 82. Polystomoides ocellatus (Rudolphi), adult worm from the anterior part of the esophagus of Emys orbicularis (L.) from the neighborhood of Poltava.

Usually the testes are located in the posterior half of the body behind the ovary but there are types in which they lie mainly in the anterior part even though some may partially extend beyond the ovary. Among Cyclobothrium sessilis (Goto) numerous testes are located in the proximity of the sex pore. Their number is more or less the same both in front of the ovary and behind it (Fig. 86). Among Diclidophora pollachii (Beneden and Hesse) the testes are located generally in the same way as in the preceeding species, but the number of testes lying closer to the anterior part is almost twice as large as those lying behind the ovary (Fig. 87). Among Octoplectanocotyle trichiuri Yamaguti, the number of testes lying in front of the ovary is also larger than those lying behind (Fig. 88). Finally, among Protomicrocotyle pacifica Meserve, all the numerous testes lie in front of the ovary (Fig. 89). The distribution of the testes in the depth p. 60
of the body varies: they either lie in the middle between the ventral and dorsal surface, or closer to the ventral side. In separate cases, the testes

are arranged into two layers, Diclybothrium armatum Leuckart (Fig. 90).

The testes are well-delineated from the surrounding parenchyma by a special connective tissue membrane. Sperm of monogenetic trematodes are usually thread-like and relatively long.

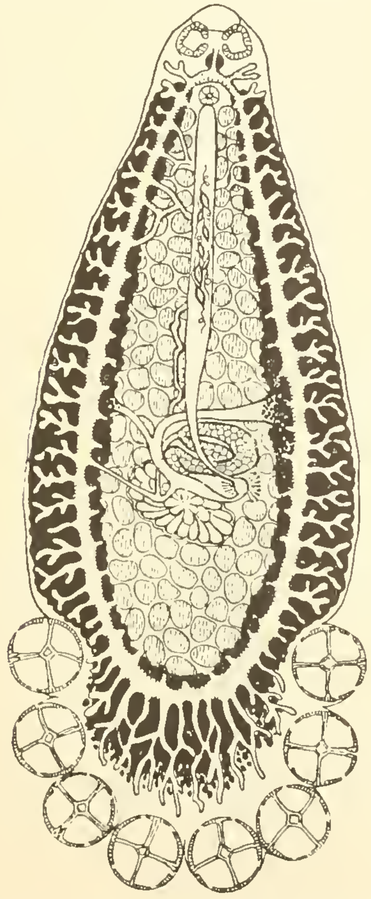

Fig. 86. Cyclobothrium sessilis (Goto), adult worm. (According to Goto, 1894).

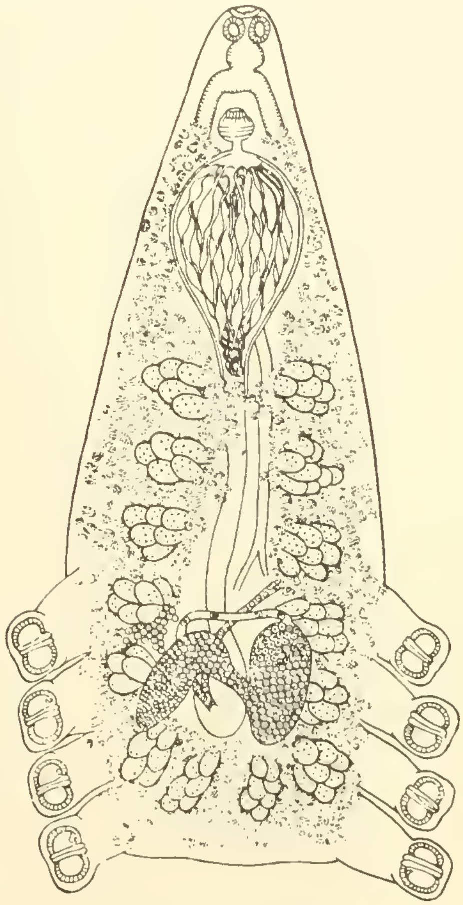

Fig. 87. Diclidophora pollachi (Beneden and Hesse), adult worm. (According to Braun, 1889-1893, somewhat simplified).

Seminal ducts are represented by efferent ducts (vasa efferentia) and by a seminal duct (vas deferens). The comparatively short little efferent canals which unite in pairs and then merge into one more or less long seminal duct emanate from the testes. Goto (Goto 1894) indicated, however, that among the highest Monogenoidea he did not see any efferent ducts and supposes that the sperm pass from one testis to another by a system of lacunae of parenchymatous origin. Among the species with a single testis, the duct which emerges from it is designated as a seminal duct. It is usually more or less powerfully twisted (serpentine, and often coiled as well, nobis) and starts from the testis at the ventral side of the body or in the middle of its thickness and quickly rising to its dorsal surface, goes to the anterior end of the body p. 61

and descends to the ventral side only in the vicinity of the sex pore. As a rule the seminal duct is single, however, in Paradiclybothrium pacificum, described by us and A. V. Gussew there are two of them (Bychowsky and Gussew, 1950). From the testis, starting at first along the ventral and then closer to the dorsal side, emerge two ducts lying along the sides of the body parallel to the intestinal trunks, now closer to the middle, now directly over them, and in front they merge into one. The reasons for the formation of two seminal ducts instead of one are not clear; however, there is no doubt that this phenomenon is secondary and quite possibly connected with the very powerful development of the uterus which, so to speak, divides the middle part of the duct.

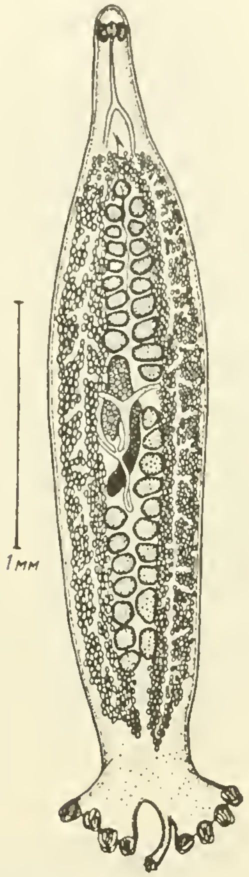

Fig. 88. Octoplectanocotyle trichiuri Yamaguti, adult worm (According to Yamaguti, 1937).

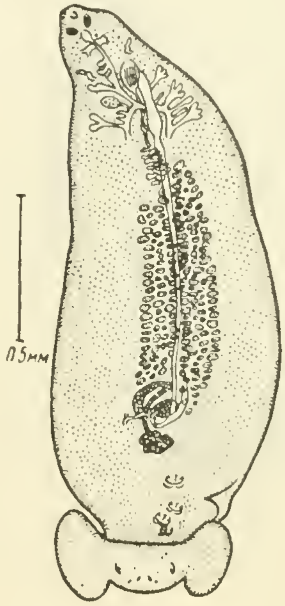

Fig. 89. Protomicrocotyle pacifica Meserve. (Combined from two drawings of Meserve, 1938).

The histological structure of the seminal ducts has been poorly studied. They are sharply delineated from the parenchyma by a special membrane toward the inside of which is located the epithelial layer with a few rounded nuclei. Apparently, at least in a number of types, there also exists a circular musculature independently under the membrane. This can be observed in Polystoma integerrimum Froelich (Fig. 91) and in a number of other forms, fresh water as well as marine.

The seminal duct passes at its terminal part into the seminal ejaculatory canal (ductus ejaculatorius) forming, for the most part, either one or several widenings of varying shape and location in front of the latter, which appear as reservoirs for the full, ripe sperm (vesicula seminalis externa).

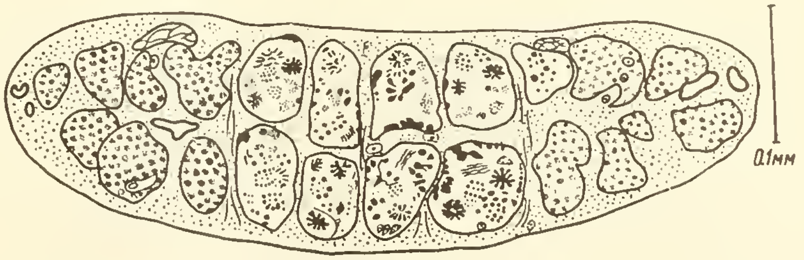

Fig. 90. Diclybothrium armatum Leuckart, cross section of the body in the region of the testes.

As a rule this ductus ejaculatorus is supplied with a sufficiently powerful musculature, it is of insignificant length and opens into the sex atrium on its terminal part, or its terminal part enters into the differently arranged copulatory organ, or finally it changes into a chitinous pipe which represents its direct continuation. In most cases a number of monocellular or polycellular glands of different origin opens into the ductus ejaculatorius. These glands are of two types, prostate and granule-containing. More often they are more powerfully developed among the forms with chitinous sex armature and weaker among those that have muscular copulatory organs. Prostate and granule-forming glands very often especially among Dactylogyridae and types close to them, form ampule-shaped reservoirs lying in direct proximity to the sex pore (Fig. 92). The physiological significance of these formations has not been elucidated so far.

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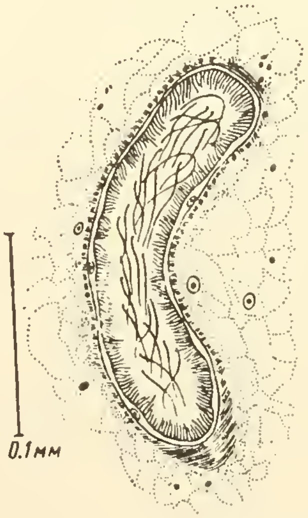

Fig. 91. Polystoma integerrimum Froelich, frontal section through the seminal duct (vas deferens).

The copulatory organ of monogenetic trematodes has a very diversified structure. Basically, one can consider two types of structures characteristic for them: in the shape of the muscular penis protruding through the sex pore, or in the shape of a completely chitinous formation. The main peculiarity in Monogenoidea is the absence among them of the turning inside out, (eversible, nobis) muscular sac enclosed in a special cirrus which is so characteristic for Cestoidea and Trematoda. All indications of the presence of cirri among monogenetic trematodes are faulty and appear as a result of inattentive study of the copulatory organs of Capsalidae in which the penis really resembles a cirrus but nevertheless, as will be seen later on, is fashioned along the type common for Monogenoidea (see however, page 476). Generally the corresponding schemes of structures of copulatory organs of Rhabdocoela can be applied wholly also to such monogenetic trematodes.

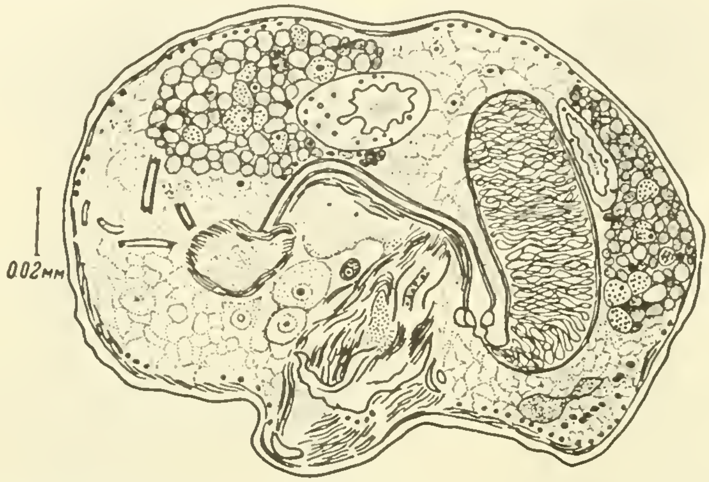

Fig. 92. *Anclyodiscoides magnus* Bychowsky and Nagibina,cross section in the region of the prostate glands.

In a more simple (from a morphological point of view) case the *ductus ejaculatorius*, representing a slightly more muscular direct extension of the seminal duct, opens directly into the sex atrium; at the same time, the role of the copulatory organ can be played by various formations not connected with these ducts and related to the sex atrium as has been indicated above. Thus, for instance, similar relations are characteristic for a number of Microcotylidae. Generally in isolated cases the sperm which falls into the sex atrium is ejected by its contraction without any special copulatory contrivances. A small muscular sucker at the end of the seminal ejaculatory canal (ductus ejaculatorius) appears as the most primitive but already isolated *copulatory organ.* (for instance among *Microcotyle caudata* p. 63
Goto, Fig. 93). This sucker is separated from the surrounding tissues by a special fold and can be extended into the sex atrium and beyond its limits through the sex pore. Morphologically it is little delineated from the surrounding tissue but has a more powerfully developed musculature, circular as well as longitudinal, further we can observe more and more the growth of the penis and also its gradual delineation from the surrounding tissues. All in all in the most complicated case (*Benedenia*, Fig. 196) the penis is completely separated by a special membrane, its upper part really lies in a spherical pocket emanating from the sex atrium and the lower part is usually spherical and inflated--or flask-shaped, in the thickness of the parenchyma. The internal structure of such a penis is sufficiently complex. The *ductus ejaculatorius* which passes through its center usually forms a more or less well-developed interior seminal vesicle (*vesicula seminalis*

interna), sometimes divided into two or three separate chambers. The ducts of the prostate and granule-forming glands enter into the body of the posterior part of the penis and sometimes they form therein reservoirs where their secretions accumulate (vesicula prostatica interna and vesicula granulorum interna). On the upper free end of the penis very often are located, in different fashion but for the most part as a corona of more or less complicated configuration, chitinous thorns or hooks which as a rule are of sharply prescribed form and of constant number in each species. p. 64

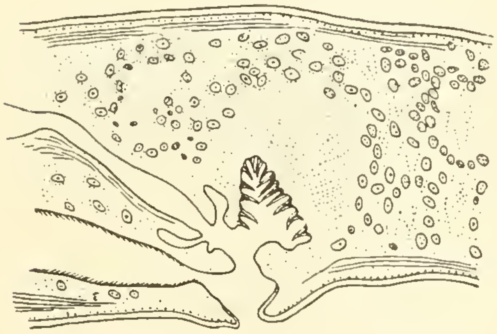

Fig. 93. Microcotyle caudata Goto, sagittal section of the body in the region of the sex aperture. In addition to the little sex sucker there is also an armed sex atrium. Enlarged 250 times. (According to Goto, 1894).

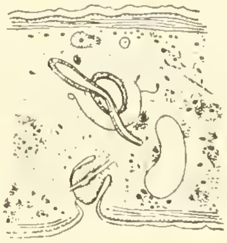

Fig. 94. Monocotyle ijimae Goto, sagittal section of the region of the sex aperture. Enlarged 140 times. (According to Goto, 1894).

Among many types as was mentioned before, the terminal part of the seminal ejaculatory duct forms a chitinous pipe which either terminates at the end of the penis or even extends beyond. In isolated cases (among certain genera) the chitinous pipe is longer than the copulatory organ and extends not only forward from it but posteriorly; very often a special muscular formation, not correlated with the penis, is located on it--bulbus ejaculatorius (as for instance Monocotyle, Fig. 94). The histological structure of the penis can become very complicated. Its musculature is usually arranged in four layers, an exterior circular--adjacent to the surrounding membrane, two

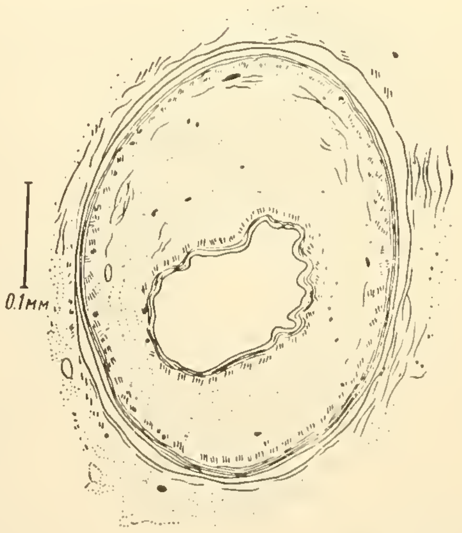

Fig. 95. Capsala sp., cross section through the copulatory organ.

longitudinal and an interior circular, lying near the ejaculatory canal (Fig. 95); the space between the musculature, the outside of the exterior membrane and the epithelium of the canal is filled by cells of the connecting tissue.

The second type of copulatory organ among monogenetic trematodes is represented entirely by a chitinous formation lying in a special envelope, and provided with separate muscular retractors (for instance, Dactylogyridae, Fig. 96). Without doubt, this type of copulatory organ originates from the chitinous armature of the pear-shaped organs of the free living flatworms as is the case among Turbellaria (Beklemeschev, 1937). The ejaculatory duct among corresponding forms is practically replaced by a special chitinous pipe into the base of which enters the ejaculatory duct and the glandular ducts--prostate and granule-forming. The formation of the pipe is mostly widened and the ejaculatory duct forms a widening seminal vesicle in its cavity. The pipe itself is of varying shape and length. Among some forms it is almost straight and broad, in others it is thin, sometimes very long, curved, and twisted completely or partially as a spiral, etc. In certain cases the diameter of this pipe, which plays — generally speaking, the role of the penis, changes along its extension very significantly, now narrowing itself toward the free end, now widening. Usually in addition to the pipe there is a special chitinous complex supporting it which is sometimes very intricately formed. The structure of the supporting apparatus and the pipe itself has a great significance in the p. 65

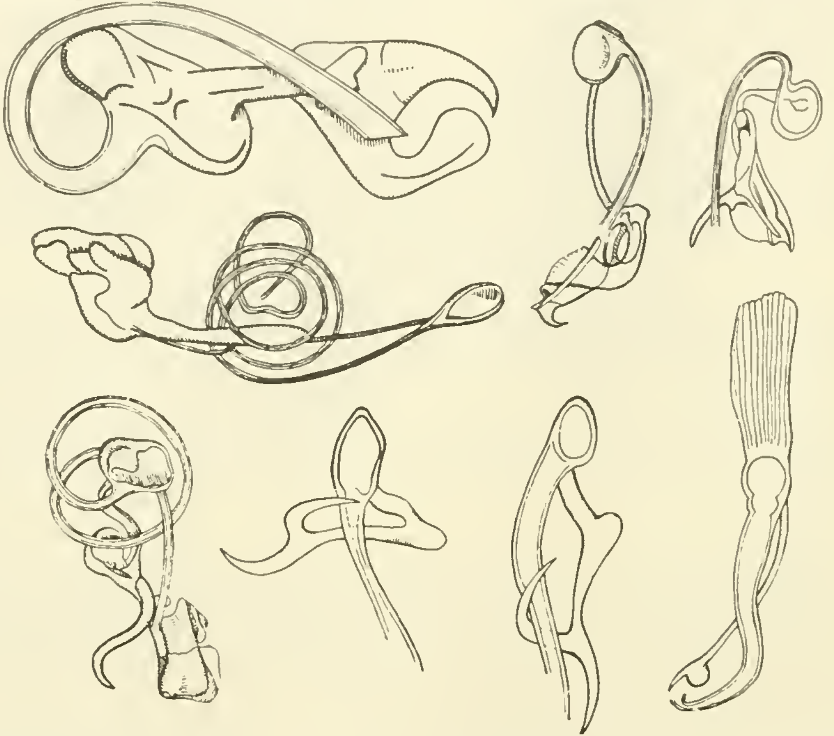

Fig. 96. Chitinous copulatory organs of different shapes, Dactylogyrus spp. Drawn at different magnifications.

systematics of a number of groups of monogenetic trematodes, appearing as a good representative diagnostic sign. For various groups of monogenetic trematodes the presence of a particular type of copulatory organ is characteristic. Thus the lower Monogenoidea--Protogyrodactylidae, Dactylogyridae, Tetraonchidae, Diplectanidae, Amphibdellatidae and others have a chitinous copulatory organ, Monocotylidae--a muscular penis usually weakly developed but often equipped with a chitinous pipe; Capsalidae and groups close to them have an unarmed penis, usually very powerful. Among Gyrodactylidae, Polystomatidae, and Sphyranuridae, a small sucker-type copulatory organ with a corona of chitinous hooks is characteristic. Among the highest Monogenoidea (Mazocraeidae, Microcotylidae and others) the penis for the most part is weakly developed, but on the other hand the chitinous hooks in the sex atrium are powerfully developed. The only genus which has no copulatory organ at all is *Diplozoon*, among representatives of which the terminal part of the seminal duct of one individual grows together with the ducts of the female sex system of the other.

The female sex system is of variable structure, differing even within the limits of a single systematic group. Basically it is represented among monogenetic trematodes by two large glands--ovary and vitelline, supplementary glands, and a number of ducts serving for the egression or excretion of the glands, for the preservation and for the reception of sperm and the preservation and egression of the eggs. As a rule all monogenetic trematodes are oviparous with the exception of one viviparous family - Gyrodactylidae. The anatomy of the female sex system of the latter is much altered in connection with the live-bearing habit and will be succintly characterized separately at the end of the description of the female sex system.

The ovary among monogenetic trematodes occurs singly and has varying shapes and sizes and in a majority of cases is located in the anterior part of the body in front of the male sex glands. In rare cases the ovary is displaced to the posterior half of the body and as an exception (for instance *Vallisia* and others) it is located behind the testes. The form of the ovary among fresh water Monogenoidea is for the most part rounded (Fig. 97A), and more seldom elongated (Fig. 97B), with a flask-shaped posterior part; whereas among the marine species the second form of ovary is the most common. Often the ovaries are strongly lengthened and significantly curved in the anterior part and in the posterior part they form not a flask shape, but a palmate shape (Fig. 97B). In certain cases the ovary is divided by a constriction into more or less equal parts. The flask type part of the elongated or the corresponding part of the round ovaries corresponds to the oögonial chamber and contains the early stages of the developing egg cells. The envelope of the ovary is of cellular structure and consists of flat, spindle-shaped cells; in the period which follows the laying of the eggs the cells of this envelope can strongly increase in size and possess the ability of seizing and p. 66
digesting the unused egg cells (see page 84).

An oviduct emerges from the ovary on the side opposite to the oögonial chamber. The latter is well isolated from the ovary, has a different structure than the envelope of the ovary, reaches a different length and ends entering the oötype.

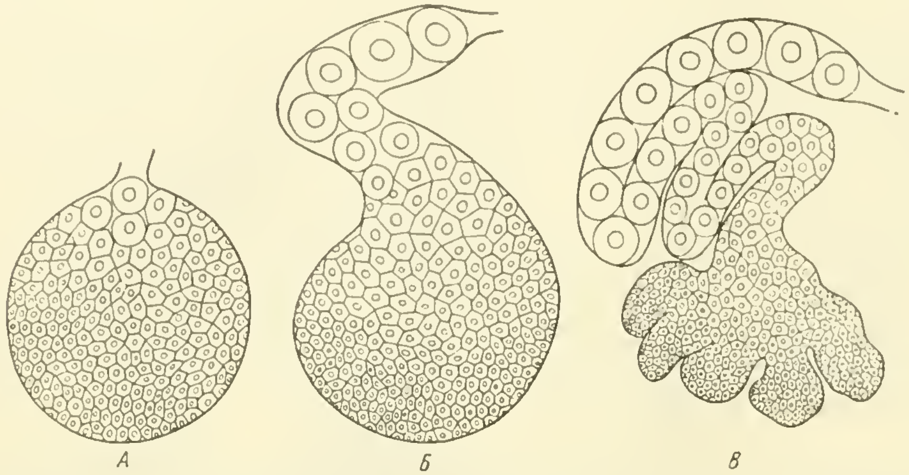

Fig. 97. Schematic representation of different types of ovaries of monogenetic trematodes. Explanation in text.

Among many Capsalidae and related forms a special chamber from which the oviduct emerges (Fig. 98) is isolated inside the ovary. This chamber apparently serves for the accumulation of a certain number of ripened egg cells before the beginning of accelerated egg laying. There is reason to believe that at the same time it can also serve as a *receptaculum seminis* inside the ovary.

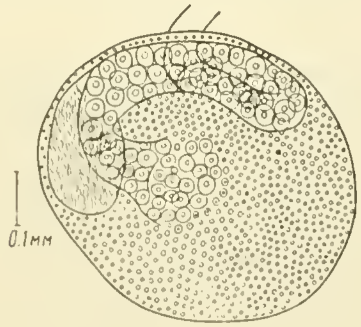

Fig. 98. *Benedenia derzhavini* (Layman), ovary with the interior chamber.

A number of ducts open into the oviduct in front of the oötype, to be specific, vitelline ducts, vaginal duct, and genito-intestinal duct. In addition to that *receptaculum seminis* also opens into the oviduct, or the oviduct itself forms a widening which is also designated as a *receptaculum seminis*. The places of junction of all of the enumerated ducts into the oviduct can be very close together and then is formed a common large cavity in the oviduct which does not have a special name, but which plays a significant role in the functioning of the female sex system, as our study has shown, (see page 85). However, it is more fitting to consider the oviduct as being divided into two separate parts. Specifically, as the oviduct (*oviductus*) must be considered that part which extends from the ovary to the place of junction with the vitelline ducts, whereas the part leading from the vitelline duct to the oötype must be designated as the female sex duct (ductus communis). Such a division is much more satisfactory because of the fact that it can also be applied to Rhabdocoela. In passing, we would also like to indicate that among various groups the number of ducts entering the oviduct varies: often the vaginal and genito-intestinal ducts or one of them can be absent. p. 67

The vitelline ducts represent the most powerfully developed part of the female sex system. These are the follicular glands; as a rule there are two, less often one or three. They are usually powerfully developed and occupy almost the entire body starting from the head end and extending to the attaching disc, and often even extending into it; the vitellaria are located between the intestines, the sex glands and the ducts and almost completely displace the parenchyma of the body. When the vitellaria are very strongly developed, they unite along the median line of the body in such a way that they have the shape of a single organ. However, even in these cases the double origin of the vitellaria is easy to establish by the presence of two efferent vitelline ducts. The latter emerge from each vitellarium one by one starting on the sides of the body; they extend mostly along the ventral side or more or less close to the medial line of the body and unite into a common vitelline duct which opens into the oviduct. Very often this unpaired or common vitelline canal forms a widening--a vitelline reservoir along its extension. The latter, however, for the most part does not reach significant dimensions.

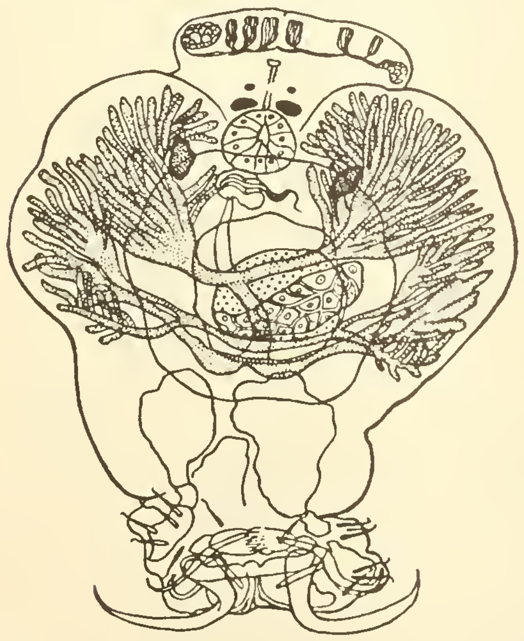

Fig. 99. Trivitellina subrotunda Johnston and Tiegs, adult worm. Natural size about 0.2 mm. (According to Johnston and Teigs, 1922).

The vitellaria are arranged in similar fashion in all monogenetic trematodes with a few exceptions. Thus, among Diplozoon, there is only one vitelline gland and correspondingly one vitelline duct (Fig. 231) because of the peculiar structure of its sex system connected with the presence of two worms grown together in its adult stage. This phenomenon is secondary. In the odd genus Trivitellina (Protogyrodactylidae) the vitellaria are divided into three groups of which each has its own independent vitelline duct, which then unites into a common one (Fig. 99, see however, page 360).

The histological structure of the vitellaria is not of special interest. We shall note that each vitelline follicle is delineated from the parenchyma by a special membrane and contains usually a small number of vitelline cells. As regards the vitelline ducts,they usually have ciliated epithelia and are equipped with a well-developed musculature which is represented predominantly by circular fibers (Fig. 100). Both help in the rapid transfer of the vitelline cells to the oviduct.

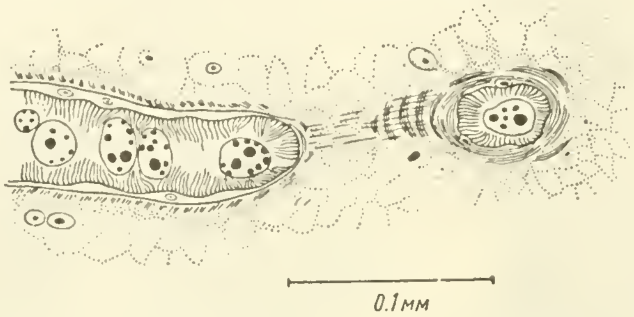

Fig. 100. Polystoma integerrimum Froelich, sagittal section through the vitelline duct.

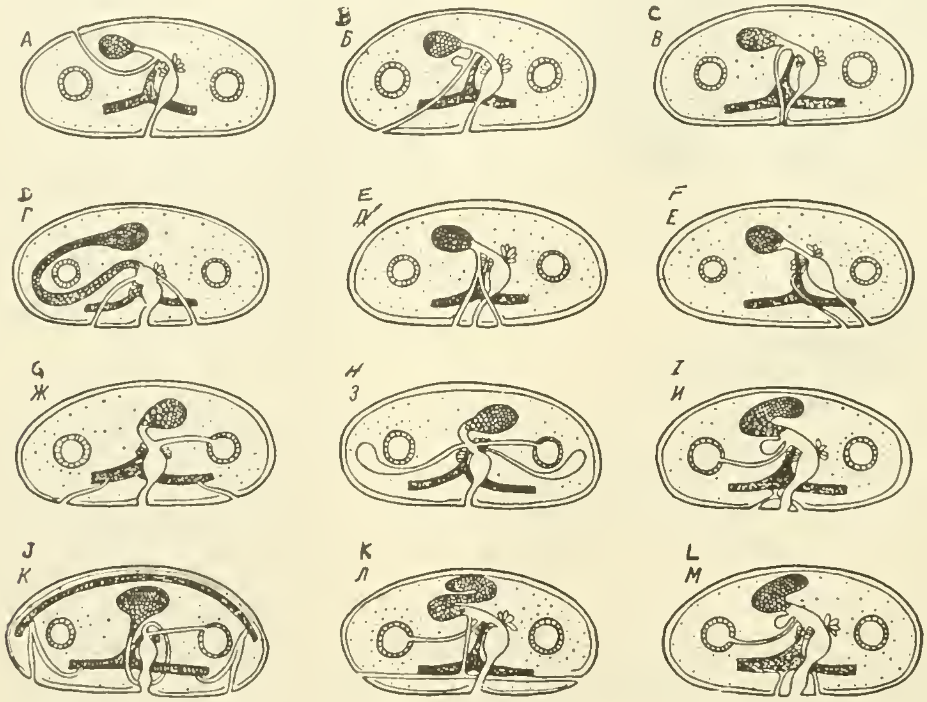

Fig. 101. Diagram of the location of the vaginal ducts among different genera of monogenetic trematodes: A--Dactylogyrus; B--Tetrancistrum; C--Murraytrema; D--Calicotyle, Merizcotyle; E--Pseudocotyle; F--Tristoma; Capsala; G--Polystoma; H--Sphyranura; I--Rajonchocotyle; J--Chimaericola; (According to Brinkman, 1952) K--Diclidophoropsis; L--Heteronchocotyle, Squalonchocotyle. (After Brinkmann, 1952).

The vaginal duct can be present or absent. In a majority of p. 68 cases it is a single duct starting from the oviduct, however, among many forms we can observe two vaginal ducts emerging, not from the oviduct, but from the vitelline ducts.

The apertures of the vaginal ducts are variously located among the different species (Fig. 101). Thus among Dactylogyridae, Tetraonchidae and other lower monogenetic trematodes, if this duct exists, it is always single and its opening lies either on the dorsal or ventral side or, most p. 69 frequently, more or less laterally. Among the types studied by A. V. Gussew "Dactylogyridae of the Hanka Lake" there is one species Dactylogyrus obscurus Gussew, among which one can suppose the presence of two vaginae; if this is so, then the secondary origin of this species is certain.

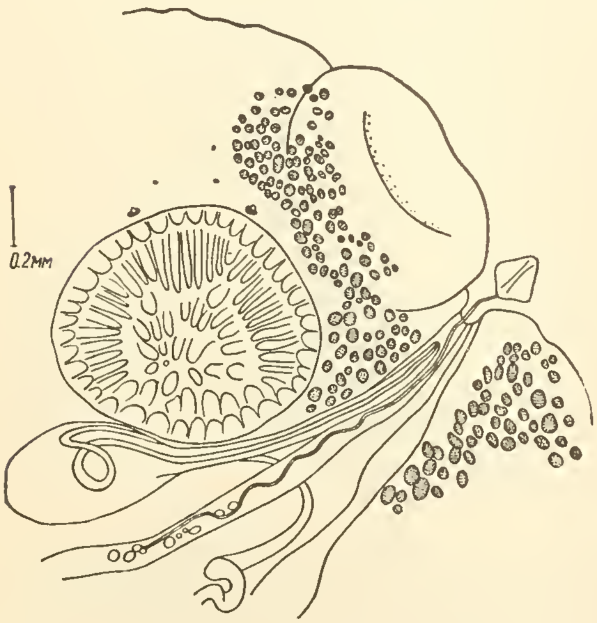

Fig. 102. Benedenia derzhavini (Layman), left edge of the anterior end of the body showing the common opening of the copulatory organ, uterus and vagina. Adult worm from the gill chamber of Sebastodes schlegeli (Hilg.) from the region of Vladivostok (Sea of Japan).

Among the Monocotylidae the vagina is single with a ventral opening in a number of forms. however, it is divided into two ducts which open independently. Capsalidae either have a single vagina or it is often absent. Its opening is located for the most part laterally in the vicinity of the sex atrium and often it even opens into the latter in the direct vicinity of the penis and the opening of the uterus (Fig. 102). Among Microcothriidae the vagina is single or double. It is interesting that in the bifurcated duct of Leptobothrium pristiuri Gallien (Fig. 103) both of its apertures open into the special organs of the sex atrium. Acanthocotylidae and Gyrodactylidae do not have vaginal ducts. As a rule they are also absent among Mazocraeidae and Discocotylidae, and if they exist they are usually single. Among Acanthocotylidae the openings are paired. It is noteworthy that in Acanthocotyle merlucci Beneden and Hesse there are two commisures uniting both vaginal ducts (Fig. 104); such a peculiarity has not been noticed in any other species of Monogenoidea. Among Microcotylidae, Hexostomatidae, and Polystomatidae the paired vaginae start from the vitelline ducts. They have either two lateral openings (Polystomatidae, and part of Microcotylidae), or they merge along the median line of the body and form a more or less elongated unpaired duct opening on the ventral side (part of Microcotylidae, Hexostomatidae). It is possible that Sphyranuridae are devoid of the vaginal ducts although according to the old data (Braun, 1889-1893) it is known that in Sphyranura osleri Wright there are two of them leading from the vitellaria but not opening outside and terminating blindly. In the given species these ducts play the role of the paired receptaculum seminis. Contemporary research (Alvey, 1933a, 1933b) subject the data concerning such structure in Sphyranura to doubts. Among the majority of Diclidophoridae the vaginal duct is absent; in rare cases it is paired, opening along the sides of the body (Diclidophoropsis). Hexabothriidae and Diclybothriidae have a divided vaginal duct which is closely connected to the vitellines and opens p. 70 by paired apertures on the ventral side or along the sides of the body. The corresponding ducts of Chimaericolidae are most interestingly arranged. They are paired, they begin from the vitelline ducts and open by two apertures on the ventral side. At the same time and somewhat lower than the external openings of each vaginal duct, there is a junction with a special transversely-oriented vitelline gland. In such a fashion each duct has two efferent openings, one internal and the other external. The physiological significance of this is completely unknown, and such a structure is unheard of in any other species of monogenetic trematodes.

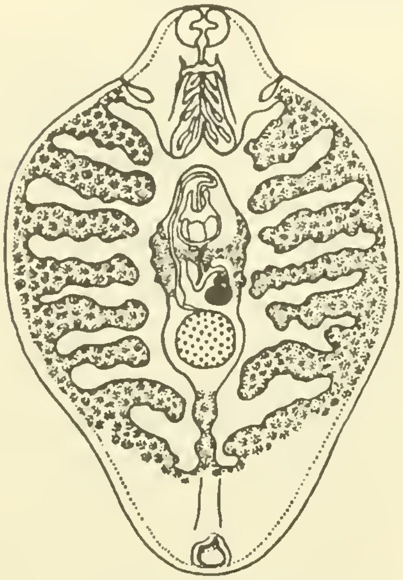

Fig. 103. Leptobothrium pristiuri Gallien, adult worm. Natural size 1.6 mm (According to Gallien, 1937).

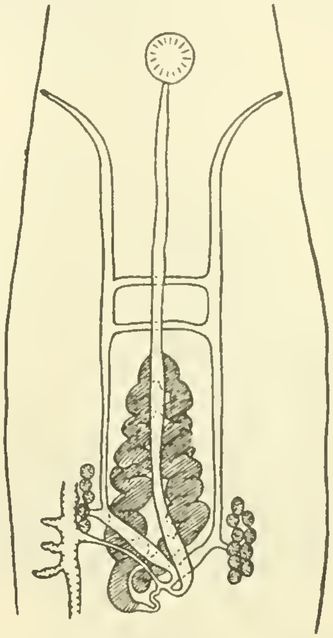

Fig. 104. Anthocotyle merlucci Beneden and Hesse, the diagram of the structure of the female sex system (According to Cerfontaine 1895, simplified).

The apertures of the vaginal tracts are often complicated. Thus, among a number of species they form sucker-shaped funnels or a conven pad, very often instead of one opening there are a number of small ones, forming in their combination so to speak a small grill (grid, *nobis*) as is observed for instance in *Polystoma integerrimum* Froelich (Fig. 71). Among many forms there is a special chitinous armature of the vaginal aperture, as for instance among many Microcotylidae (Fig. 105). Finally, among many of the lowest Monogenoidea the terminal portion, which is sometimes a very significant part of the entire vaginal duct, has the shape of a small chitinous pipe or funnel (Fig. 106).

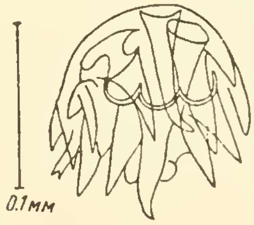

Fig. 105. *Microcotyle* sp. from the gills of *Sebastodes schlegeli* (Hilg.) from the region of Yablochnoii (Southern Sakhalin, Sea of Japan).

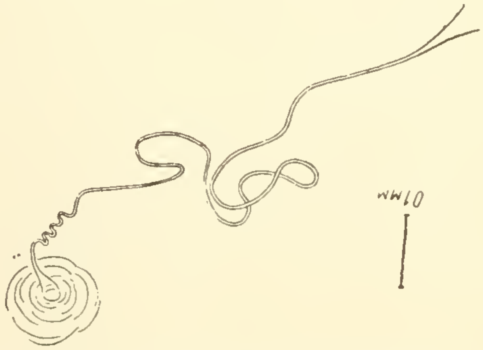

Fig. 106. *Ancylodiscoides magnus* Bychowsky and Nagibina, from the gills of *Silurus glanis* L. from the Delta of the River Volga. Chitinous armature of the vaginal duct.

The genito-intestinal canal (*canalis genito-intestinalis*) exists in Polystomatidae, Sphyranuridae and all Oligonchoinea. In its structure this duct is somewhat reminiscent of the vitelline glands and also equipped with a ciliated epithelium and circular musculature, starts from the oviduct and extends, having greater or less length, and because of this being more or less curved, toward one of the intestinal trunks into which it opens. Sometimes however, the *canalis genito-intestinalis* opens into one of its transverse branches and not directly into the intestinal trunk. Among Protogyrodactylidae one observes a very odd-shaped peculiarity in the structure of the female sex system which appears as a distinguishing sign of that family. According to the description of Johnston and Tiegs (Johnston and Tiegs 1922), the vitellaria of these forms have a junction with the intestinal trunks near the anterior end of the body which can be designated as the vitello-intestinal duct (*canalis vitellario-intestinalis*). This formation undoubtedly is completely unique and cannot be considered homologous to any duct of the other Monogenoidea (see however page 360). p. 71

On the question of the homology of the *canalis genito-intestinalis* and all of the vaginal ducts of flatworms, there exists considerable literature in which are expressed the most varied points of view. According to one of them, the vaginal duct of Monogenoidea is homologous to the one in Turbellaria and Cestoidea and to Laurer's canal of Trematoda, whereas the *canalis genito-intestinalis* of Monogenoidea is similar to the one among Turbellaria. These points of view, with certain alterations, are held by Bresslau (Bresslau, 1928-1933) and Reisinger (Reisinger, 1923) and also Fuhrmann (Fuhrmann, 1928) and a number of other researchers. Others, as for instance Goto (Goto, 1894) and Looss (Looss, 1893), consider that the vagina of Monogenoidea corresponds to the uterus of Cestoidea, whereas the *canalis genito-intestinalis* corresponds to Laurer's canal of trematodes. Finally, a well-known authority of digenetic trematodes, Odhner (Odhner, 1912-1913) supposes that the vaginal duct of Monogenoidea is not homologous among the various species and that the vaginal duct emanating from the ovary represents the true vagina and that the duct emerging from the vitelline reservoir or from the vitelline ducts is a *sui generis* formation which he designates as the *ductus vaginalis*. In connection with this, Odhner considers that the *ductus genito-intestinalis* corresponds only to the true vagina of Monogenoidea and also Laurer's canal of Trematoda. The system of Monogenoidea (see further page 336) proposed by Odhner appears to be the result of this point of view.

We think that the vaginal duct of Cercomeromorphae is a formation homologous to that among Turbellaria. Also from our point of view the homology of the *canalis genito-intestinalis* of Monogenoidea and Turbellaria cannot be subjected to any doubt. p. 72 As for the comparison of the *canalis genito-intestinalis* and the vaginal duct with Laurer's canal of Trematoda it appears to us more reasonable to compare the latter with the vaginal tract of Cercomeromorphae. The views of Goto and Looss on the homology of the vagina of Monogenoidea and the uterus of Cestoidea do not withstand serious criticism. There is no doubt that it is a result of their being carried away by the convenience of comparison of the interrelations of the ducts of both groups, but this point of view cannot be recognized as correct. Finally the point of view of Odhner has, at first glance, a serious basis; however, in the light of the present level of knowledge of Monogenoidea this view appears erroneous. The fact is that he established two suborders of Monogenoidea (which he accepts as an order). These two suborders, Monopisthocotylinea and Polyopisthocotylinea, differ by the fact that in the second there is a *ductus genito-intestinalis* (vagina) and *ductus vaginalis*, whereas among the former there is only a vagina, however, as Fuhrmann correctly points out, we encounter among the first group of Odhner those relations which this author consider characteristic only for the second group. Thus, for instance among *Tristoma* there is a *ductus vaginalis* according to the terminology of Odhner, but there is no *canalis genito-intestinalis*. We noticed similar relations among a number of other Capsalidae and among part of Monocotylidae and so forth. Undoubtedly, it is possible to find almost all transitions between the typical vagina according to Odhner and ductus vaginalis. Because of this we have no right to consider these formations as not homologous and consequently Odhner's point of view also appears to be erroneous. The receptaculum seminis occurs among representatives of all groups of monogenetic trematodes. Often however it is also absent. It represents a special widening which serves for the retention of sperm and its location is varied. Sometimes it is simply a widening of the oviduct. In a number of species the receptaculum seminis lies along the vaginal duct or is even functionally replaced by widening sections of the latter. There are no designations for the various types of receptacula seminis, however, one must recognize the receptaculum seminis oviducti and the receptaculum seminis vaginalis as not homologous formations.

The oötype into which the ductus communis passes represents the place of the formation of the eggs. Usually it is powerfully developed and separated from the duct which opens into it and also from the uterus, if the latter exists, by powerful sphincter-shaped muscular fibers. The form of the oötype varies, it can be rounded, egg-shaped, pear-shaped, etc., which basically corresponds to the shape of the egg which is formed therein. This oötype can be considered as an odd-shaped mold for the "stamping" of the eggs. Into it open numerous monocellular glands called shell glands or Mehlis' glands. Among a majority of species they are sharply developed and often divided into two groups which are variously colored on the slides. This can be observed with special clarity among Polystoma integerrimum Froelich. The function of these glands is not completely clear (for more details on this see pages 85 and 87).

Among a number of Monogenoidea the oötype opens directly into a sex cloaca and the egg which is formed passes from the oötype, after a certain period of time, into the surrounding medium without prolonged delay in the body of the parasite. In other forms a more or less long uterus, which contains the fully formed eggs for a certain time, starts from the oötype. In such a fashion among some forms, the oötype functionally serves as the uterus and in other types as both. One must note that this peculiarity does p. 73 not have important phylogenetic significance. Apparently the absence of the uterus is a primary phenomenon but among a number of forms, even highly organized ones, there is only an oötype. It is interesting that, during the time of embryological development of Polystoma integerrimum the so-called "gill form" has only an oötype, whereas the form from the urinary bladder of the frog has a well-developed uterus (see page 185).

The uterus can be of variable length from comparatively short to very long and very curved and in a majority of species its curves lie across the body and only in Chimaericola are located longitudinally (Fig. 107). Among many forms the uterus is sac-like. Characteristic among some is the distribution of the eggs in a packet, whereas among the majority they are arranged one after the other. The histological structure of the uterus is similar to that of the oviduct.

For the convenience of description the structure of the eggs is described in the chapter on embryology (Fig. 89). The only viviparous family, Gyrodactylidae, sharply distinguishes itself from all other Monogenoidea by the structure of the female sex system. The most studied sex system is that of Gyrodactylus (Fig. 12). This genus is characterized by presence of the ovovitellaria ("Keimdotterstock" of the German authors) and the absence of vitelline glands. Also in connection with this, the egg cells of Gyrodactylus, in contrast to all other monogenetic trematodes, are fairly richly supplied with yolk although the feeding of the embryo which is developing within the uterus takes place apparently basically by way of the liquid alimentary substances which penetrate from the body of the worm into the uterus. Besides the indicated peculiarities, among Gyrodactylus the vaginal and genito-intestinal canals are also absent. Undoubtedly the simplified structure of the sex system of these species is a secondary phenomenon and even the presence of the "ovo-vitellaria" which often occurs among Turbellaria, should not be considered as a primary primitive peculiarity.

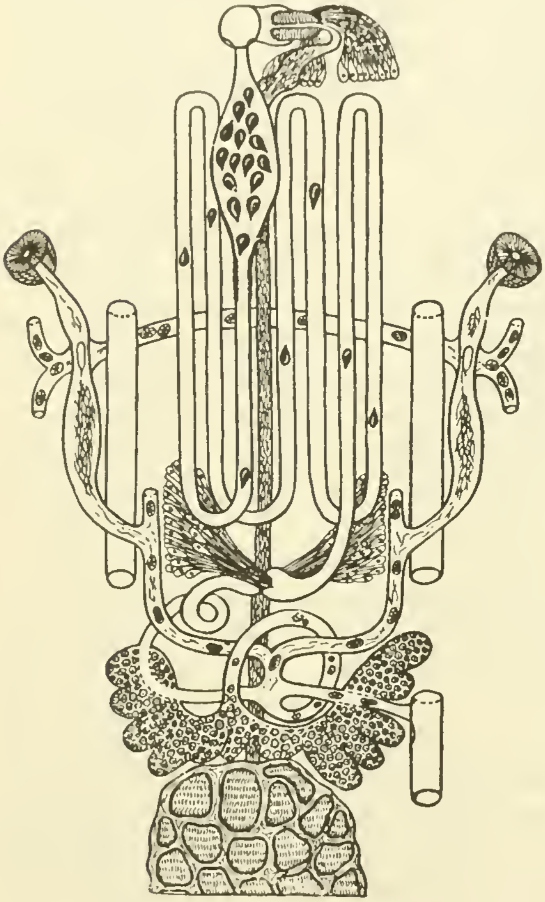

Fig. 107. Chimaericola leptogaster (Leuckart), diagram of the structure of the sex system (According to Brinkmann, 1942).

In conclusion, it is necessary to note with regret that the level of the morphological study of monogenetic trematodes is still very low which undoubtedly hampers attempts at formulating a system to a significant measure.

CHAPTER II

BIOLOGY OF MONOGENETIC TREMATODES

The locations of monogenetic trematodes are quite diversified. As is known, they parasitize mainly sharks, skates, holocephalans and bony fishes, amphibians and reptiles, and in addition, parasitic isopods, and are also known to exist on cephalopods and aquatic mammals. p. 74

The parasites of fishes are found on the gills, in the gill chamber and buccal cavity, on the surface of the body, on the fins, in the cloacal cavity and in its vicinity, in the ureters and the body cavity, and finally, as an exception, in the heart. The majority of monogenetic trematodes parasitize the gills and may be located very differently thereon. A majority of the species occur on the gill filaments, a few species of Gyrodactylus are located on the gill rakers, and a number of Monocotylidae and Capsalidae on the lateral surfaces of the gill arches, mainly on Elasmobranchii.

The parasites which occur on the gill filaments are distributed differently. First of all, many forms occur on all four gill arches of the fishes and five to seven arches of the shark-types whereas others locate on the second and third arches in most cases or even exclusively. Thus, as a rule, a number of species of Mazocraeidae do not occur on the fourth arch and very seldom occur on the first, even in the case of relatively high levels of infection. Different species have favored places of location within the limits of a single gill arch. Some species (many Dactylogyridae and others) are located along its entire length, while others are either located only in the middle (for instance Diplozoon), or at either end (on the anterior end, for instance Monocotyle and the posterior, Nitzschia). Likewise the location in relation to the length of the gill filaments varies among different species. Thus, as a rule, Dactylogyrus anchoratus Dujardin settles at the base of the gill filament, whereas Dactylogyrus vastator Nybelin, on the other hand, settles at their very tips. Very often "concomitant" (terms of V. A. Dogiel) species of Diplectanidae, Mazocraeidae and others can be easily distinguished by their location on the gill filaments.

Monocotylidae and Capsalidae live mostly in the gill and buccal cavities. Representatives of the genera Benedenia and Capsala and others which live in the gill chamber usually are located on the interior surface of the operculum near the posterior bases of the gill arches. The worms locate differently in the buccal cavity. Thus, for instance, Nitzchia sturionis (Abildgaard) occur in the lips, the palate, the tongue and sometimes even in the beginning of the esophagus, and certain Monocotylidae--quite to the contrary--live only on the surface of the palate.

Many species are encountered on the surface of the body, among
these are Microbothriidae, many Monocotylidae and Capsalidae, Acantho-
cotylidae and a number of Gyrodactylidae. The latter settle mainly on the p. 75
surfaces of the head, whereas Acanthocotylidae settle on the ventral and
dorsal surfaces of the body. Monocotylidae and Capsalidae settle on either
side, more or less indifferently, whereas Microbothriidae settle, apparently
preferably, on the dorsal sides of the body of their hosts.

Many lower Monogenoidea, mainly Gyrodactylidae and more rarely Dactylogyridae live on the fins. In addition, Calceostomatidae certain Microbothriidae and also, where found, Monocotylidae and Capsalidae usually act as parasites on the fins. The species which act as parasites of the fins occur more often on the pectoral, than the dorsal, and more rarely on the caudal, ventral, and anal fins. Calicotylinae inhabit the rectal cavity and its vicinity among shark-type and holocephalan fishes. Until the present time only three species of *Acolpenteron* parasites of Cobitidae, Catostomidae and Centrarchidae were discovered in ureters.

The special monogenetic genus *Dictyocotyle* (*D. coeliaca* Nybelin) parasitizes the body cavity of certain types of skates.

Until the present time the only type found in the blood system is *Amphibdella torpedinis* Chatin. Ruszkowski (Ruszkowski, 1931), studying *Torpedo ocellata* Ruszkowski and *T. marmorata* Risso at the Naples Zoological Station, found adult worms in eight specimens of the first species (or about 35 per cent of those examined) and eggs in twelve individuals (or about 50 per cent); among *T. marmorata* only eggs were discovered in the heart. In this connection numerous worms were found in the normal habitat, that is the gills. Ruszkowski supposes that either the larvae which emerge from the eggs, penetrate into the blood system and there reach maturity and then lay their eggs while the newly acquired larvae perish or the adult worms penetrate the blood stream (with the help of the head glands ?) and there remain without changing morphologically, but adapting themselves to the new conditions. Indisputably, one must consider such location aberrant.

The parasites of amphibians and reptiles, i.e., representatives of Polystomatidae and Sphyranuridae, settle on the skin, gills, buccal cavity, under the eyelids and in the urinary bladder. The only species indicated for mammals, *Oculatrema hippopotami*, Stunkard, was described from the eye of a hippopotamus (see page 219). The parasite of cephalopod mollusks -- *Isancistrum loliginis* Beauchamp lives in the gills of *Loligo media* Linné.

Representatives of Diclidophoridae are encountered on parasitic Isopoda (for instance *Choricotyle charcoti* (Dollfus) on *Meinertia oestroides* or *Choricotyle smaris* Ijima on the caudal segment of *Cymothoa* sp. sp.); however, we are not inclined to consider these cases as specifically parasitic action because the same types of Diclidophoridae are encountered on the gills of fishes which are the hosts of these Isopoda.

As a rule monogenetic trematodes locate on the body of their host by attaching themselves by the posterior ends, and in normal conditions have little relocation movement or even do not change their location at all. Many species, however, are completely deprived of the ability to transfer,either because of a special structural arrangement of their attaching apparatus, or as a result of the growth of tissues of the host which surround the part of the body of the parasite and finally attach the worm for its entire life to a fixed position (Fig. 108). Under certain conditions, mainly unfavorable ones, many of the small worms (Dactylogyridae, Tetraonchidae and others) as well as the large worms (Monocotylidae, Capsalidae and others) move along the body of their host fairly actively. This transfer takes place with the help of the attaching apparatus of the posterior and p. 76 anterior ends, and resembles the locomotion of leeches. The worm, which starts to move, first attaches by its anterior end,having stretched it in the direction of movement, and then, having attached itself, draws the entire body to the anterior end, again attaches itself by the posterior end, and repeats the same motion (Fig. 109). It is not without interest to note that the strength of attachment of monogenetic trematodes by means of the anterior and especially the posterior end is very great. Thus, Dactylogyridae, which have been isolated into a saltshaker (some type of experimental vessel--perhaps similar to a stender dish?, *nobis*) and which have attached themselves to it, withstand a fairly strong stream ot water from a pipette; apparently the attachment results from a sticky secretion of the glands from the posterior end of the body because the hooks cannot play a significant role under such conditions. Certain large forms, for instance *Nitzschia sturionis* (Abildgaard), which have a powerful sucker attach themselves with such force that it is easier to tear the worm in two than to pull it from its place of attachment.

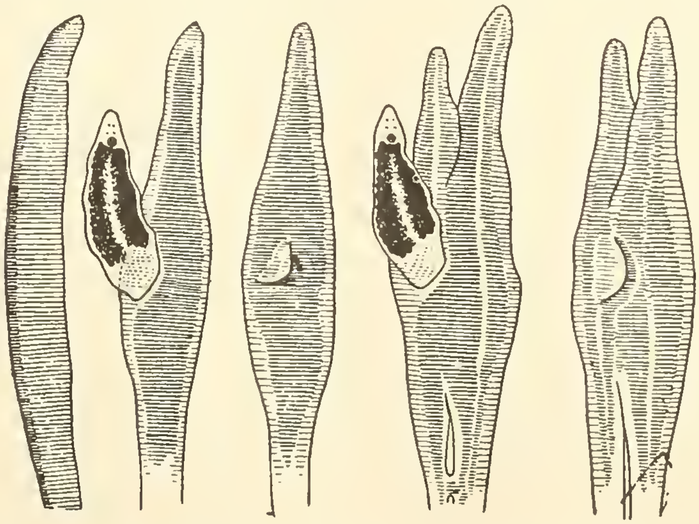

Fig. 108. *Dactylogyrus iwanowi* Bychowsky, adult worm sitting on the gills of *Leuciscus brandti* Wal. from the region of Vladivostok (Sea of Japan). On the left normal gill filament.

In the latter case and cases similar to it, it appears that the basic role is played by the cavity which is created as a result of the contraction of the muscles (in the posterior attaching apparatus, nobis) and which has less pressure inside than outside. This is substantiated on the one hand by the swelling which remains on the body of the host (after the worm detaches or is detached, nobis) similar to the ones resulting from medical jars (suction jars, nobis) and on the other hand by the fact that if a very thin capillary, which allows passage for the water from the outside, is placed under the disc of the attached worm, there is little difficulty in removing the worm, and in most cases it will fall off itself.

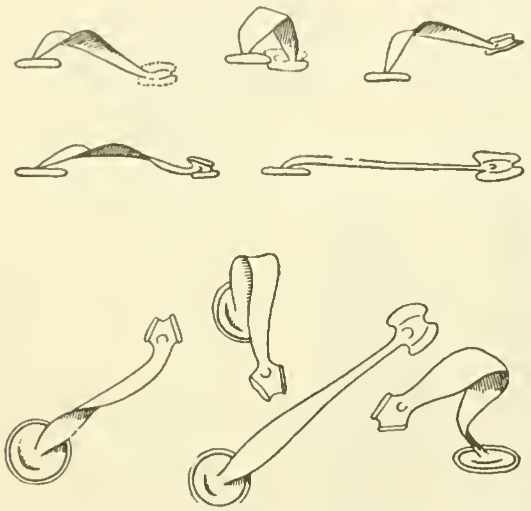

Fig. 109. Nitzschia sturionis (Abildgaard), locomotion of the worms along a flat surface. Sketches made on the Island of Sara (Caspian Sea) from the worms discovered in the buccal cavity of Huso huso (L.).

Certain sections of the dissertation of N. A. Izumova (1953) were dedicated to the questions of behavior among monogenetic trematodes on the gills of their hosts. While studying the influence of the oxygen content of the water on Dactylogyrus solidus Achmerow and D. vastator Nybelin, she succeeded in showing that the change in the quantity of oxygen in the container leads to a change in the location of the first of these types. Thus, with a decrease in the oxygen content of the water D. solidus actively move to the ends of the filaments of the first and fourth gill arches concentrating on their ventral sections--places of the best aeration and conversly with an increase p. 77 in the oxygen content the worms return to the places of their original location, that is, to the middle and lower parts of the filaments of the second and third gill arches. The data of Izumova show that this is connected with the conditions of aeration of the different sections of the gills. As regards D. vastator, the change of oxygen supply does not cause a change in the location of the worms; apparently these worms are much less demanding of conditions of aeration.

The species which are not capable of motion because of special arrangements of attaching apparatus, are encountered mainly in the highest Monogenoidea, but they are also present among the lowest. Thus, Diplectanum similis Bychowsky, which parasitizes near the bases of the gill filaments of Corvina nigra Salv., has such a distribution and arrangement of connecting pieces of the middle hooks of the attaching discs that it is deprived of the possibility of active transfer (movement, nobis) and at best can only detach itself from one gill filament and attach itself to a neighboring one. Many Microcotylidae with a large number of attaching clamps are practically devoid of the ability to transfer, although the separate clamps can easily change their position. As a matter of fact, among these species the adhesive glands of the posterior end are completely undeveloped and they are not in a condition to attach themselves to smooth glass surfaces with their posterior ends. This applies to the adult individuals, wnile the young ones still possess attaching capability.

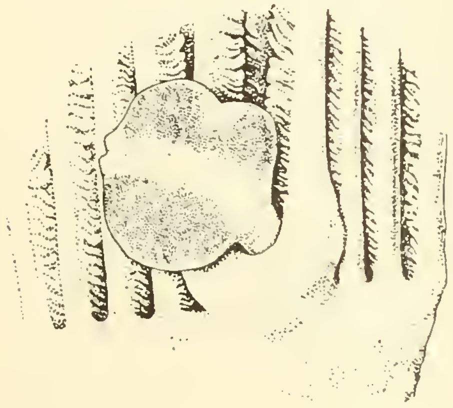

Fig. 110. *Linguadactyla molvae* Brinkmann, adult worm on the gills of *Molva dipterygia elongata* from the south of England (Atlantic Ocean). Natural size of worm about 3 mm.

The reactions of the host to the attachment of monogenetic trematodes can be very different. With the attachment of worms by means of hooking apparatus, we often observe significant injuries to the body of the host. On the gills of fishes strongly infected by Dactylogyridae, one can easily notice numerous hemorrhages and ulcerations of the epithelium. It was already mentioned that during the attachment by means of the discs, large round bruises and swellings are formed. At the same time, significant ulceration of the tissues of the host also takes place in serious cases of this type. The highest monogenetic trematodes which attach themselves by means of clamps apparently inflict the least damage. In a number of cases the irritation of the tissues of the host under the influence of the presence of the worms will cause growth of epithelium and connecting tissue, as a result of which significant swellings develop. With this, among a number of hosts the tissues will grow over and around the attaching disc of the worm, and among some, special growths are formed on which the parasite remains and these growths often fall off carrying the worm with them, and in this fashion, clear the parasite from the host. We see examples of fixation by the tissues of the host among *Dactylogyrus iwanowi* Bychowsky (Fig. 108) and *Linguadactyla molvae* Brinkmann. The second type of changes of the tissues of the host

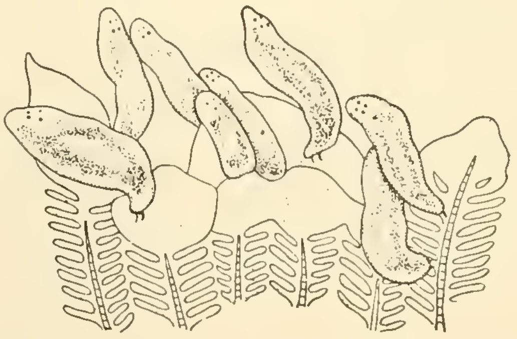

Fig. 111. *Dactylogyrus vastator* Nybelin, adult worms on the gills
of the carp, forming pathological p. 78
growths. Magnification 30 times. (According to Wunder, 1929).

is easily observed in mass infestations of the young of cultured carp by *Dactylogyrus vastator* Nybelin (Fig. 111). Pathological changes under the parasitical action of monogenetic trematodes can bring with them a very dangerous character for the host. We know that with a strong infection many species of Monogenoidea can cause death of the host, and under very unfavorable conditions (e.g. overcrowding of fishes, etc.) can also even cause mass epizootics which have great significance in pond culture of fishes. Thus, in Silesia numerous epizootics of carp caused by *Dactylogyrus vastator* Nybelin caused millions of losses to pond farms. A very well-known serious incident of the mass destruction of the small Aralsk sturgeon in a natural reservoir (occurred, nobis) as a result of insufficiently planned attempts at acclimatization of the stellated sturgeon in the Aralsk Sea which carried *Nitzschia sturionis* (Abildgaard), which was never encountered there before, with it into this reservoir (or body of water, *nobis*). (For greater detail see Lutta, 1940). There is reason to believe that during the attempts at acclimatization of Gwiniads (Gang Fish, nobis) the *Discocotyle sagittata* (F. Leuckart) which parasitize them can cause undesirable epizootics.

The incidence of occurrence of parasites on their hosts is still very insufficiently known for a majority of monogenetic trematodes. It is not something constant for each species, but depends on a number of various factors: geographic situation of the region of research, the location of the latter in the range of the host, or the time of the year, or the biology of the host, etc. Very often the parasite which is encountered on 100 per cent of the hosts in the main portion of the range of the latter is encountered very seldom near the edge of the range. For instance, *Dactylogyrus simplicimalleata* Bychowsky in the Delta of the Volga is encountered in 100 per cent of the hosts, while in the Bay of Finland it is a great rarity. *Ancylodiscoides siluri* (Zandt) in the lower part of the Volga is encountered on 100 per cent of the Sheetfish (*Siluris glanis*, *nobis*), whereas above Seratov it is encountered only in rare cases. For the most part the majority of representatives of Dactylogyridae are encountered on 100 per cent of the fishes in the middle of the range of the host in the summer, and in the winter, as a rule, not p. 79
more than 20 to 25 per cent. On the other hand, among the same family a number of species are very rarely encountered throughout the year, as for instance *Dactylogyrus similis* wagener on the Roach of the Leningrad region. For many Monogenoidea the incidence of occurrence changes to a great degree depending upon the age of the host. Thus, numerous *Gyrodactylus* which parasitize 100 per cent of the young fishes are discovered in the adult only in exceptional cases. *Protancyrocephalus strelkowi* Bychowsky is a typical juvenile parasite of the flounder, among the young of which it occurs in 100 per cent of the cases, whereas it is practically absent among the adults. On the other hand, many monogenetic trematodes are completely absent in the young individuals of the host and infest the adult fishes in large percentages. Thus, *Diclybothrium armatum* Leuckart is not encountered on young sturgeon and very often occurs on from forty to eighty per cent of the adults. According to our studies, this parasite is not encountered on Sterlets

20 centimeters in length, on Stellated Sturgeons up to 45 centimeters in length, on Sturgeons up to 43 centimeters in length; according to the data of Dubinina (1952) and of 184 Sturgeons and 161 Sterlets measuring up to 40 centimeters from the lower part of the Volga, only 1. 7 per cent were infected. Apparently the largest individuals were the most infected. In the autoreference of N. L. Nichiava's dissertation (1953) there is an indication that 52. 94 per cent of the young Sterlets examined in the region of Seratov were infected with D. armatum. Unfortunately the author does not indicate the sizes of the fishes; it is thought that she had relatively large fishes -- which become infected first in natural conditions. Only young individuals of herring and mackerel which are completely devoid of Monogenoidea come to the Barents Sea near the region of the Murmansk Biological Station, whereas the adult individuals living near the shores of Norway and England are intensely infested by Mazocraes and Octostoma. It would have been possible to show a significant number of similar examples but we shall only indicate further that the dependence on the incidence of occurrence of the age of the host was well examined on Polystoma integerrimum Forelich by Zeller (Zeller, 1872a). His researches, which were done at the same time in a single place, showed that frogs aged from 6 to 7 months are 90 per cent infected; that those aged one and one-half years, 33. 3 per cent; those two and a half years old, 42 per cent; and those three and a half years, 27 per cent; and those four and one-half years, 10 per cent.

The salinity of the water exercises great influence on the incidence of occurrence. Thus, in the freshened part of the Aral Sea we found Dactylogyrus simplicimalleata Bychowsky in 80 per cent of the cases and in strictly marine water--40 per cent, whereas in fresh water--93. 3 per cent. Interesting studies were conducted by us on the lakes of the Barabinskaya Steppe (Bychowsky, 1936a). The influence of salinity on the incidence of occurrence of Dactylogyridae on the fishes was clearly apparent. It was indicative that in the most saline parts of Bolshoi Chan and Mali Chan, the monogenetic trematodes were almost absent. Moreover, the only finding of Dactylogyrus nanus Bychowsky on Bream in Bolshoi Chan showed, during the checking of the material, that the infected individual of the fish had a different tempo of growth than all the others and undoubtedly came to Bolshoi Chan very recently and had not succeeded in freeing itself of the parasite. However, side by side with the species which change incidence of occurrence depending upon the salinity, there are also species which behave quite indifferently to it. These are a number of species of Gyrodactylus parasitizing the Three-spined Stickleback which is infected by them both in fresh and ocean water. In addition to the existing direct observations on a number of regions, S. S. Shullmann conducted very informative experiments at our request. He transplanted sticklebacks infected with Gyrodactylus sp. sp. from fresh straight into sea water and observed that after a short period p. 80 of "salt-shock" the worms continued normal movement and apparently did not experience any harmful consequences. Reverse experiments in retransplantation of fishes and worms from the sea into fresh water gave the same results. We should also note that many species occurring on various hosts have varying incidences of occurrence for each one which is fully within the law (normal, natural--in conformity with the established natural law or principles, nobis). Thus, Ancyrocephalus paradoxus Creplin is discovered in a considerable percentage on Lucioperca and in a very small percentage on Perca. The incidence of occurrence of Nitzschia sturionis (Abildgaard) on the White Sturgeon or Beluga (Huso huso, nobis) is always significantly higher than in the Stellated Sturgeon, Sturgeon and Small Sturgeon (Acipenser stellatus, Acipenser, and Acipenser nudiventris, nobis).

The intensity of infection of Monogenoidea fluctuates extremely among the various types. Certain species are encountered mostly in a few individuals per host, whereas others occur by the thousands on a single host individual. For instance, within the limits of one genus Gyrodactylus; G. marinus Bychowsky and Poljansky are encountered on Cod in the Pacific Ocean by the thousands per host, whereas G. groenlandicus Levinson is encountered on Bullhead (Cottus) only in a few individuals per host.

The clarification of the factors which influence the incidence of occurrence should be considered very desirable because it will be possible in this connection to establish rational measures controlling illnesses caused by them under conditions of pond culture.

There is almost no information concerning the life span of monogenetic trematodes. What is known without a doubt is that along with the forms which live less than a year (a majority of Dactylogyridae, Gyrodactylidae), there are numerous types which live several years. Thus, Dactylogyrus iwanowi Bychowsky lives not less than two years, which is evident from its life cycle (see page 110). Diplozoon paradoxus Nordmann begins to lay eggs only in its second year and apparently lives not less than a year after the first laying. Mazocraes alosae Hermann, which parasitizes Caspian herrings, infects the fish at the age of not less than a year plus, and perishes together with the host at the age of two to three years during the death of the fish after spawning. Polystoma integerrimum Froelich which infects frogs only in the tadpole stage, is often encountered among frogs which are six years old and thus lives not less than five to six years under favorable conditions. On the other hand, a form of this same P. integerrimum which lives in the gills of tadpoles in the semi-adult condition (see page 121) has a life span of not more than one and one half to two months. On the basis of the data of life cycles on Monogenoidea, one can expect that generally the majority of the highest forms have a polyannual existence, although this is not significantly substantiated by specific observations. The continuity of life of the commercially important Dactylogyrus vastator Nybelin has not been fully elucidated up to this time in spite of numerous studies of its biology. According to the experiments of N. A. Izumova, which were recently carried out, the normal span of life for the majority of D. vastator fluctuates between 25 and 40 days, however, it must be taken into consideration that certain individuals without a doubt live through one winter and consequently perish at the age of not less than 6 to 7 months.

The span of life of monogenetic trematodes after the death of the host is generally not great. We happened to discover live worms on dead fishes not later than 24 hours after the death of the host. Usually monogenetic trematodes do not abandon the body of the host under any conditions, but certain species from the skin and fins possess this capability. Thus, according to our observations, many *Gyrodactylus* leave the fish after certain periods and for 12 to 14 hours move in lively fashion along p. 81 the bottom of the reservoir (or container, *nobis*). It is possible that they are not deprived of the ability to infect new individuals of the host. As regards the survival of the worms in artificial conditions without food (in salt shakers with constantly replenished and aerated water), the periods are also insignificant. Bear (Bear, 1827) shows that *Nitzschia sturionis* (Abildgaard) lives not more than 24 hours; this form lived somewhat longer -- up to 30 hours -- in our experiments. According to Thaer (Thaer, 1850), *Onchocotyle appendiculata* (=*Squalonchocotyle* species, according to present nomenclature) lives in water not more than 36 hours. *Capsala molae* (E. Blanchard) can live in water without food up to 14 days (Braun 1889-1893), *Diplozoon paradoxum* Nordmann from 3 to 9 days (in the last case, by being fed with fresh fish blood). Dactylogyridae, Gyrodactylidae, and Polystomatidae live not more than 48 hours in water (without food). Usually they perish at the end of 24 hours.

Feeding of monogenetic trematodes takes place on the body of the host and at its expense. During the time of feeding, the worms customarily attach themselves by the anterior end and less often perform scraping motions. Among the majority of forms the seizure of food takes place mainly with the help of the pharynx, more seldom of the buccal funnel or buccal suckers. As has already been indicated, the pharynx is capable of protruding in a manner resembling the pharynx of Turbellaria; usually it is equipped with a number of powerfully developed glands which apparently play a role in the preparation of food before its seizure inside the digestive system. As food, monogenetic trematodes use epithelial cells of the covering of the host, secretions of the glands, and blood. Part of the species feed by all, and some only by one of these types of food. For the most part Dactylogyridae feed on the mucous secretions of the skin and its cells, although a number of species, as for instance *Dactylogyrus vastator* Nybelin, Tetraonchidae, Calceostomatidae, Monocotylidae, certain Tristomidae and other families close to them feed preferably on the blood; Gyrodactylidae, almost exclusively on mucous and epithelial cells; Polystomidae and Sphyranuridae, mainly on the blood. Numerous highest Monogenoidea also feed pre-eminently on the blood. The egestion of undigested food remnants takes place also through the buccal opening and apparently after indeterminant periods following reception of food.

The reproduction of monogenetic trematodes can take place during fixed (or limited, nobis) periods, or it can be more or less extended in time. As a rule reproduction does not take place during the winter among fresh-water forms, whereas among marine forms this occurs in a number of cases. The majority of Dactylogyridae and Tetraonchidae apparently reproduce more or less steadily during the course of the entire warm period, but the conditions of temperature and oxygen diet influence the tempo of reproduction to a great extent. Thus, under existing conditions of the middle of the European U. S. S. R., common species of Dactylogyrus, Ancyrocephalus and Tetraonchus produce eggs beginning from April up to September and, depending upon the nature of the year, much later. We do not have any data about the time of reproduction of Monocotylidae and Microbothriidae and a number of other Polyonchoinea. According to our data, Capsalidae reproduce mainly during the first half of the summer months. The presence of embryos among Gyrodactylidae is observed all year round, although their birth is apparently adapted to the warm months. Among the highest species, a part reproduces during all the summer months, and some also in the winter months, whereas others have a fixed period p. 82
connected with the peculiarities of the life cycle of the parasite and of the host. For instance, among Polystoma integerrimum Froelich the reproduction takes place only during a very short period (directly after the emergence from the places of hibernation), and lasts about a month -- at the latitude of Leningrad from the end of April to the beginning of May (sic). The gill forms of Polystoma integerrimum reproduce during the entire period of its maturity until the end of life, which coincides with the end of the metamorphosis of the tadpoles, that is, one and one half to two months Let us note that the species which reproduce periodically and, in this connection which lay a relatively much larger number of eggs in a short period of time than the species with extended laying, in a majority of cases have a longer or more voluminous uterus, sometimes containing a great number of eggs (among P. integerrimum more than 100 eggs, among Microcotyle gotoi Yamaguti up to 150). For more detailed information concerning reproduction see pages 105-137.

Among species with extended periods of fertilization, the activity of the male sex system takes place more or less steadily during the entire warm period of the year. Among such species during that time we always find all or almost all stages of spermatogenesis in the testes, and in the seminal ducts and in the vesicula seminalis a greater or lesser number of ripe spermatozoids ready for fertilization. Among species which have a more or less short period of fertilization the male sex system acts periodically. Thus, among P. integerrimum increased spermatogenesis begins in the period which follows the laying and ends at the end of the summer, and at that time almost the entire testis and partially also the vas deferens is filled with ripe spermatozoids. The latter are preserved in this shape until spring and during the period of fertilization are almost completely used up. During the time of fertilization the vas deferens among Polystoma is strongly inflated from the mass of spermatozoids which fills it to excess. During all the remaining time it is strongly narrowed and its interior lumen almost completely declines. The prostate glands are also more intensely filled during the period of reproduction.

The fertilization of worms is achieved through cross- or self-fertilization. Cross-fertilization can occur by means of copulation or without it. Among Monogenoidea which have vaginal ducts insemination occurs through them; among forms without vaginal ducts, just as among digenetic trematodes, it takes place through the uterus. However, the possibility that certain types with vaginal ducts can also be inseminated through the uterus is not excluded. Copulation of Monogenoidea is known only among a small number of species because of the difficulty of observation. This process has been studied best of all among *P. integerrimum*. Their copulation takes place in the period directly preceding the egg-laying and sometimes during it. Both worms taking part in copulation remain attached to the urinary bladder wall, they embrace with the anterior ends and alternately introduce their copulatory organs into one or the other of the vaginal apertures and during an hour there can be twenty copulations. The role of the male and of the female is alternately borne by both: now one plays the role of the male, and the other of the female, now the reverse. Because among *Polystoma* the vaginal apertures on each side of the body are in the shape of a sieve plate, the copulatory organ cannot be fully introduced into them but only its chitinous hooks. The period of individual acts of copulation is rather significant: it lasts from one-quarter to one-half minute. Zeller (Zeller, 1876) observed the process of copulation of *Polystoma* and so did we. We have conducted special experiments, the methodology of which is not without interest. In order to observe the behavior of p. 83
Polystoma in natural conditions we immobilized the frog and then opened its ventral cavity, placing the operated animal into a little bath of physiological solution. After the opening of the ventral cavity we introduced the physiological solution by pipette through the anal opening into the bladder in such quantities that the bladder would be fully distended and as a result completely transparent. The *Polystoma* contained therein was studied under the binocular microscope and the observations could be conducted up to 48 hours without any noticeable deterioration in the condition of the host and of the parasites.

Wilde (Wilde, 1937) described copulation among *Dactylogyrus macracanthus* Wegener. It lasts from fifteen to twenty minutes and takes place after the worm which acts as the male has already laid its eggs. The worms are seldom observed *in copula*. During copulation a spermatophore is introduced into the vagina and the *receptaculum seminis* is filled with sperm. However, in spite of numerous attempts we never succeeded in observing the copulation of different types of *Dactylogyrus*; as a result of this we are inclined to think that this process takes place not as simply as it is described by Wilde, and probably is of a different nature.

Cross-fertilization without the help of copulation (this method was first indicated for digenetic trematodes by Sinitsin in 1906) can take place among certain species living in the regions of low concentration and their spermatozoids are ejected from the copulatory organs of one individual of the parasite and reach the sex glands of the other through the surrounding medium. In addition to that, there is reason to believe that a number of species form spermatophores (apparently many Dactylogyridae, and apparently a number of highest species).

Self-fertilization among Monogenoidea occurs very often in all families. It takes place either by means of self-copulation (this, however, is subject to doubt), or without copulation by means of cross-fertilization through the surrounding medium. Certain species are mainly self-fertilizing (for instance *Dactylogyrus iwanowi* Bychowsky), while a large majority has recourse to this method only where cross-fertilization is impossible. Thus for instance during the presence of one parasite in the urinary bladder of the frog (and this can be almost in 50 per cent of the cases of infection *Polystoma integerrimum* Froelich), the copulation which we just described fertilizes itself, and no delay in egg-laying or abnormal development of eggs has been noticed.

The adaptation to cross-fertilization among *Diplozoon paradoxum* Nordmann is completely different. The adult forms of this species are encountered only grown in pairs in a criss-cross fashion. In them the ducts of the female sex system of each individual grows together with the ducts of the male sex system of the other so that for the entire life the possibility of cross-fertilization is insured and conversely self-fertilization is excluded (Zeller, 1872b). The same peculiarity is possessed by other species of the genus *Diplozoon*. Apparently, nevertheless, cross-fertilization occurs much more often than one can suppose and, of course, than can be observed. It can be guaranteed by the alternate ripening and development of male and female sex products, which was observed by a number of authors. Thus, Sproston, (Sproston, 1945b) saw this among *Octostoma scombri* (Kuhn). She considers that among the worms there are at least three phases during their lives when the male system acts predominantly and two when the female predominates. As a rule the male system begins to function first; our data also substantiate this.

The functioning of the female sex system falls into a number of p. 84
successive phases. Thus the activity of its separate parts takes place, now during the time of the reproductive period, now beyond it, and finally in both. As an example of the activity of the female sex system we shall analyze it among *Polystoma integerrimum*, a specie which was especially studied by us for a number of years. Everything that will be said further about this can be extended to the remaining Monogenoidea, with the exception that among species with an extended period of laying these stages can coincide in time and part of them, specific for *Polystoma*, is completely excluded.

Toward the period of egg-laying which begins after the winter months, the ovary of *Polystoma* from the urinary bladder of the frog is in a condition of full readiness for the mass discharge of ripe egg cells. It is almost completely filled with them and only a small intensely-pressed chamber near its upper end which is slightly curved is filled with cells in various stages of oogenesis and these are in the "frozen" condition, unchanging for a long period. The envelope of the ovary during this time is thin and membranous. Its separate cells are noticeable only with great difficulty. Just before the very beginning of egg-laying, a process called by us "excision" of the eggs takes place when the egg cells change from the polygonal, as they are during the winter period, into the rounded shape. During the "excision" of eggs not the entire cell is rounded (?, *nobis*), a part is rejected and completely taken,out as a rule through the genito-intestinal duct into the intestine. The reasons and significance of this rejection of a part of the cells are completely unclear to us. During the time of the laying the ovary frees itself of a large mass of egg cells, in connection with which it even changes its shape to a more extended one. Toward the end of egg-laying only sex cells which begin to develop strongly remain in the ovary,and they are in different stages of oögenesis. In addition, a certain number of oöcytes which were not ejected remain in the ovary after the laying, as a rule in large or smaller quantity. The process of increased oögenesis, which begins at the end of the laying, continues during the entire summer and terminates in the fall before the departure of the frogs for hibernation. At this time the ovary acquires the same aspect as before laying and remains in this condition until the following reproductive period, that is until the spring of the following year. Parallel to the process of oögenesis, immediately after the laying an increased process of degeneration of unused oöcytes takes place. They gradually fall apart and are seized by the cells of the envelope of the ovary which develop strongly at that time and in which the remnants of the oöcytes are digested. The process of degeneration and seizure of the remnants of the egg cells by the envelope was observed by us among species with long reproductive periods, as for instance *Nitzschia sturionis* (Abildgaard). During the period of egg-laying the vitellaria, which develop extremely powerfully and occupy the main part of the animal, quickly expend the vitelline cells, and after that they develop intensely again during the summer and toward the winter they are already in the ready state among *Polystoma*. Among species with an extended period of laying, the expenditure and replenishment of the vitelline cells takes place at the same time. During the period between layings, all the ducts of the female sex system are in the deflated state and empty, whereas during the period of egg-laying they are strongly swollen because they contain some other fluid in addition to the sex products (see further). After copulation the sperm enters into the strongly inflated middle section of the vaginal ducts which among *Polystoma* functionally replace the receptaculum seminis of other forms (it is interesting to compare it with the blind vaginal ducts of *Sphyranura* which play the same role; see ,however,page 69). The expenditure of the sperm and of the vitelline and egg cells in forming the eggs takes p. 85

place gradually and is regulated on the one hand by the muscular widening of the oviduct which is located at the place of junction with the vitelline duct and which plays the role of a valve in front of the ootype, and on the other hand by means of extrusion of excessive sex products into the intestine through the genito-intestinal canal. Apparently this extrusion should be considered as the basic and only function of the latter. All the sex products, which in the oötype are surrounded together in determined portions by a shell and in the shape of eggs, are transferred into the uterus from which, after a relatively short time, they are extruded. The function of the uterus is clear; it serves as a place for the preservation of eggs which have not yet been completely formed or hardened and besides, among forms with "rationed" laying, and to that type Polystoma is related, as the place of collection of a determined number of eggs which are set aside at the same time. One must also remark about "shell" glands which forcefully extrude their secretions into the oötype around which they are located during the period of laying. Toward the end of the laying their contents are completely emptied and replenishment takes place gradually during the summer period. The significance of the "shell" glands nevertheless remains unclear. As was already indicated (page 72) they consist of two groups and consequently produce two different secretions -- liquids. If one can suppose that one represents fluid which fills the ducts and so to speak "lubricates" the sex products contained therein and first of all the eggs, then what is the function of the second? One can only think that, in spite of the existing views (see Goldschmidt, 1909), this secretion plays a certain role in the formation of egg cells (for more details see page 87).

We should also indicate that among species without the genito-intestinal canal, the unused sex products are also extruded but through the uterus and they are thrown completely outside without any utility for the organism. In very rare cases, especially during the disruption of the activity of the sex system, we observed that unused sex products are extruded through the uterus, and among species with the genito-intestinal canals, particularly among Polystoma. Thus, summing up the data concerning the function of the sex system in Polystoma, we see that it takes place so to speak in three phases falling into definite periods: preparation for laying, the period of laying itself, and the "post-laying" recuperative period. We see such a distinct periodicity among the large majority of Monogenoidea which have polyannual existence; and among other species one observes the overlapping of one phase with the other and all the processes are more extended in time.

CHAPTER III

DEVELOPMENT OF MONOGENETIC TREMATODES

As was indicated, the formation of eggs takes place in the oötype p. 86
and the speed of their formation can sometimes be considerable. Thus, according to our observations, the time during which an egg is formed among *Dactylogyrus vastator* Nybelin fluctuates from 4 to 20 minutes, whereas among *Polystoma integerrimum* Froelich this period is sometimes decreased to one and one half minutes. The number of eggs deposited by a single individual monogenetic trematode is very great; this is true in equal measure of the species with short life spans as well as those with long ones. Thus, among a number of species of *Dactylogyrus* the egg deposition continues almost the entire summer, and it is more or less uniform during this time. Very interesting are observations in the deposition of eggs of *D. vastator* which were conducted by N. A. Izumova. According to her very meticulously executed experiments, it was found that in surroundings which approach natural conditions *D. vastator* deposits eggs very intensively but not uniformly depending upon the age and the oxygen conditions of the milieu. Generally, we can expect that at normal oxygen levels worms which begin laying at the age of eight days after attraction to the host deposit from 4 to 10 eggs in a period of 24 hours at 12° to 18° C during the first ten days. A decrease in oxygen and a rise in the water temperature result in an increase in the number of eggs deposited. That is why it is so easy to acquire an intensive laying of *D. vastator* in artificial and obviously unfavorable conditions.

Among *Polystoma integerrimum* Froelich, according to our observations in natural conditions, the eggs deposited during the spring egg-laying period reach 2,000 to 2,500 and on separate days the number fluctuates from a few to 1500. As observations indicate, certain individuals of *P. integerrimum* produce eggs more or less uniformly through a number of days, and others deposit at first a large number of eggs and then their laying is quickly curtailed and then completely stops. It is apparent from Table 1 which way the process takes place among different individuals which are found in the host singly and among several parasitizing the frog at the same time. The egg-layings, the data concerning which are given in the table, took place under experimental conditions at an earlier time than in nature, but their nature fully corresponds to this process under natural environmental conditions.

The process of egg formation among monogenetic trematodes can be considered as almost completely unstudied. During the observations of development of eggs among *Dactylogyrus* we often"had eggs with already formed but still soft shells containing only the egg cell. These eggs had open posterior ends and into them were poured, after a certain time, vitelline cells and this infusion was accompanied by intense contractions of the p. 87

TABLE 1

Deposition (oviposition, nobis) of Polystoma integerrimum Froelich in "natural" conditions[1]

Data (1928-1929 r.)	t°	Frog No. 2 Worm No. 3	Frog No. 3 Worm No. 8	Frog No. 5 Worms No. No. 24-32
18 XII	15	-	-	-
19 XII	16	75	1500	-
20 XII	15	175	230	-
21 XII	15	150	75	5 (0-1)
22 XII	15	100	100	370(41)
23 XII	16	900	75	1850(205)
24 XII	15	255	30	860(95)
25 XII	16	100	15	1250(138)
26 XII	16	125	10	1150(127)
27 XII	16	120	-	1100(122)
28 XII	15	110	-	650(72)
29 XII	15	70	-	1000(111)
30 XII	15	80	-	700(77)
31 XII	15	30	-	550(61)
1 I	14	-	-	50(6)
2 I	15	-	-	90(10)
3 I	14	-	-	30(3)
4 I	15	-	-	10(1)
5 I	15	-	-	-
Total deposited		2290	2035	9665
Deposited by one individual		2290	2035	1074

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[1] Numbers in brackets refer to the number of eggs per one sample of parasite.

vitelline ducts. Very often, separate vitelline cells return to the vitelline ducts with the contractions of the uterus. After a certain period the eggs close, and at the place of the opening remains a little foot of the egg which lies behind the uterus at the place of junction of the vitelline ducts. In such a fashion, as much as can be ascertained by these intermittent observations, the little foot of the eggs of *Dactylogyrus* appears not as an individual specially formed outgrowth but corresponds to the wall of the egg pressed and elongated like the "little nose" of an electric bulb," (Bychowsky, 1933). Views similar to the one described were observed in a number of other monogenetic trematodes, fresh water as well as marine. However, there is still much that is not clear. In the beginning, in the oötype the shell of the eggs, as is obvious from the preceding, has a soft consistency and only after a certain time hardens. This was noticed earlier by a number of researchers. Thus, Kulwiec (Kulwiec, 1927) writes that the egg of *Dactylogyrus anchoratus* (Dujardin) in the oötype (uterus by her terminology) is soft and during the contractions of the body changes its shape.

There are different opinions concerning the formation of the egg shell. Some authors (predominantly of the last century) think that it is formed at the expense of glands which are now designated as Mehlis gland and formerly called shell, and others that the shell is formed at the expense of the "shell" secretion of vitelline cells and that the secretion of the "shell" glands is of no, or in extreme cases, of very little significance in this process. p. 88 The last point of view, substantiated by certain histological studies, appears to be more or less generally recognized at the present time. It appears to us, however, that this question cannot be considered as finally settled. First of all, there are no sufficient bases to maintain that the egg shell and its derivatives, that is the little foot and filament (see further page 90), are fully and always homologous. If this (explanation, *nobis*) is quite possible for eggs with a small foot and filament, on the other hand, it is easier settled negatively for the eggs with complex and strongly developed derivatives. Thus in the sections through fully formed eggs of *Acanthocotyle verilli* Goto, we see (Fig. 112) that the envelope of the egg is colored somewhat differently than the posterior part of the little feet which apparently are formed at the expense of a different secretion than the envelope itself. In the formation of eggs of *Diplectanum aculeatum* Parona and Perugia, one can likewise observe that this process is sufficiently complex. The uterus is filled with a liquid which is possibly produced by the shell glands even before the formation of the egg. At first, the egg cell gets into the uterus and then the vitelline cells. The vitelline cells enter the uterus by portions and immediately after they appear in the narrowed first part of the uterus, the egg shell begins to form. After the cessation of the influx of the vitelline cells and the formation of the shell, at the posterior end of the latter there remains an opening into which several vitelline cells pass back into the narrowed anterior part of the uterus. At this time around the cells which have come out, a little foot begins to grow further and further from the end of the egg in the shape of a hollow little pipe. Then the moment comes when these vitelline cells fall apart, so to speak, and disappear and at this time the formation of the little foot ends. Its lumen is reduced either completely or in certain places, leaving small cavities. At that time the little foot is still lacking the little end star which is characteristic of the eggs of *Diplectanum*. The latter begins to form after the final formation of the little foot and apparently at the expense of some other secretions not connected with the vitelline cells. In this fashion, there is reason to believe that the egg shell is formed not only at the expense of the vitelline cells, but also at the expense of other secretions. These can only be produced by the "shell" glands, because there are no other glands in the female sex system. However, one must recall, as was indicated (see page72), that the "shell" glands themselves are not homologous but consist of unicellular glands of different structure and probably producing a different secretion.

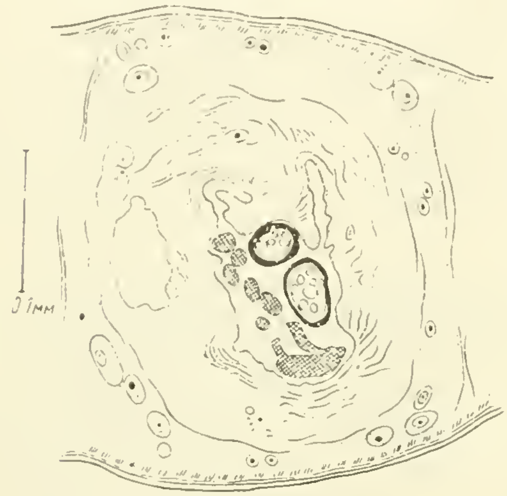

Fig. 112. *Acanthocotyle verrilli* Goto, cross section in the region of the uterus. Two sections cut through the eggs, and pieces of the little feet of the egg are seen in the uterus. Worms from the skin of *Raja radiata* Don. near the region of *Murman* (Bering Sea). Explanation in the text.

p. 89 In the work of A. V. Ivanov (1952) on the structure of *Udonella caligorum* Johnston the oötype and the glands which enter it are described in significant detail and the author talks convincingly about indisputable participation of the secretions of one type of "shell" glands in the formation of the envelope of the egg. We are inclined to think that this opinion can be substantiated by our data for monogenetic trematodes. Likewise, the data of A. V. Ivanov concerning the complex structure of the little stem of the egg of *Udonella*, which is the equivalent of the little foot of the eggs of Monogenoidea, fully corresponds to the data about the formation and structure of the little foot of *Diplectanum*, *Nitzschia* and other monogenetic trematodes. In connection with this, one must say that the similarity between *Udonella* and Temnocephala indicated in the work of A. V. Ivanov by the characteristic of the gluing of the egg to the substratum by this secretion, which differs from the substance of the egg envelope, should be extended also to Monogenoidea because it is a characteristic which is common for all three groups. The formed egg consists of the envelope with its derivatives, of a relatively small number of vitelline cells, and of an egg cell against which the spermatozoid comes tightly. The latter usually lies without change until the deposition of the egg, because the fertilization of the egg cell takes place later and only in rare cases at the time of the presence of the egg in the maternal organism.

The shape of eggs of monogenetic trematodes is very different. It varies from almost spherical, oval or egg-shaped to pyramidal and even more complex (Fig. 113). As a rule, the shape of the egg depends upon the configuration of the inner surface of the oötype and represents, so to p. 90 speak, a molding in accordance with its form. The eggs of Monogenoidea can be easily oriented because on the upper end there is a more or less noticeable operculum. In a majority of forms the eggs have offshoots of the shell located on the upper, lower or both ends. The majority of researchers group all of these sprouts under the common name, filaments of the eggs. In our opinion this is completely inaccurate because the upper and lower sprouts are formed differently and are not homologous to each other. We designate the sprout of the upper pole of the egg as the filament and the lower as the little foot. The little feet of the eggs can be very short in the shape of a small thickening at the anterior end of the egg (a majority of Dactylogyrus); its location can be varied; either precisely along the axis of the egg, for instance Ancylodiscoides siluri (Zandt), or it can be more or less considerably displaced (for instance among Dactylogyrus wegeneri Kulwiec). The short feet are for the most part straight and devoid of

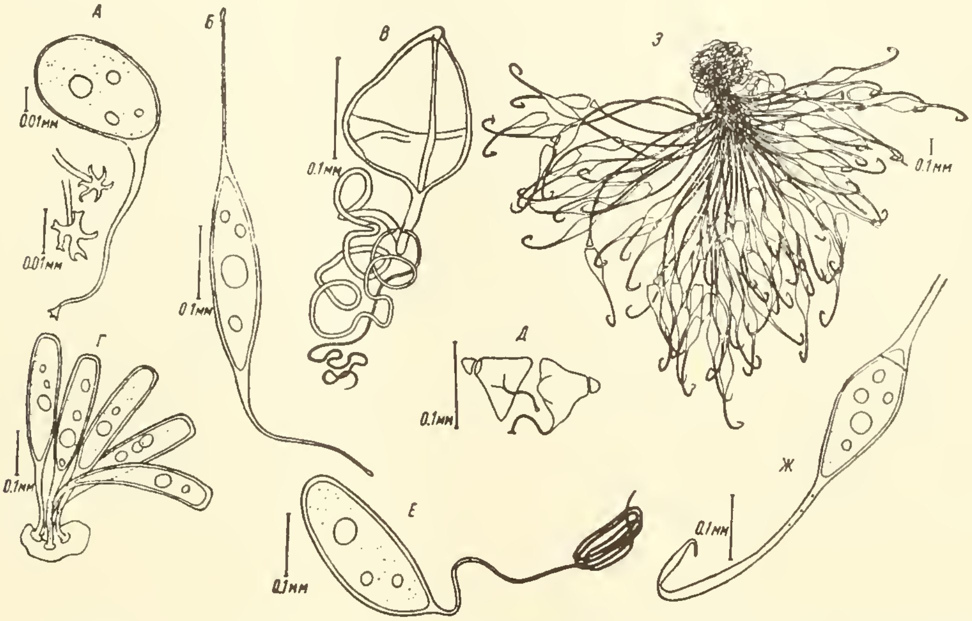

Fig. 113. Eggs of monogenetic trematodes. A--Diplectanum aucleatum Parona and Perugia (under the egg, the end feet of two eggs, greatly magnified); B--Mazocraes alosae Hermann; C--Benedenia derzhavini (Layman); D--Acanthocotyle verrilli Goto, group of eggs (with common bases!); E--Protoancyrocephalus strelkowi Bychowsky; F--Diplozoon paradoxum Nordmann; G--Microcotyle gotoi Yamaguti, deposition (mass, nobis) of eggs; H--Microcotyle gotoi Yamaguti (entire mass is deposited at one time!).

thickenings or widenings at the free end (for instance *Ancyrocephalus*). The longer feet can be of various lengths, sometimes they can even exceed the length of the egg several times (many *Microcotyle*), usually they are equipped with a noticeable widening -- a little platform at its free end. This little platform can be of an irregular shape (many Dactylogyridae), or it can acquire a completely regular outline, as for instance among *Diplectanum* with a regularly 5- to 6-pointed little star at the end of the little foot of the eggs. In a number of cases the end of the little foot forms a sharply curved, hook-shaped growth (for instance among *Microcotyle gotoi* Yamaguti). Usually the little feet of the eggs, which have a considerable length are more or less strongly curved and, more rarely, are completely straight. The filament of the egg is of the same shape as the little foot. In a number of cases it is shorter than the little foot (for instance among *Mazocraes*), or more often it is absent (majority of the lowest Monogenoidea). However, among many marine types it is filiform and exceeds the combined lengths of the egg and the little foot (many *Microcotyle*). In certain cases, the filament of the egg forms a small widening at its free end. Among a number of species (for instance among *Microcotyle caudata* Goto), the little foot of one egg fuses with the filament of another forming, in such a fashion, a little chain of a varying number of eggs. Oftener the feet of individual eggs merge together into a common foot of several eggs (for instance Acanthocotyle). Finally, sometimes the filaments of the eggs can also become agglutinated to each other (certain *Microcotyle*). The color of the eggs varies from bright yellow to dark brown. Usually the color changes from a lighter to a darker shade at the time of formation and further development of the egg.

Among different species the sizes of the eggs fluctuate from 0.02 to 0.18 mm without including the length of the little feet and the filaments. The latter may be many times (more than 60) the length of the egg itself. In a number of cases the sizes of the eggs can vary greatly within a single species. Thus, in *Dactylogyrus vastator* Nybelin we have observed eggs from 0.074 to 0.126 mm in length, that is the linear increase of size was almost double and the volume even more so.

The manner of deposition of eggs of monogenetic trematodes can be divided into two groups, the first deposits eggs into the water and they fall onto the bottom or onto different objects on the bottom; the second produces eggs which attach themselves to the body of the host or become stuck in the mucous which surrounds the location of the parasite. To the first group are related forms wherein the little feet and filaments of the eggs are absent or, on the contrary, those which possess powerfully developed offshoots from the eggs but which predominantly deposit eggs in groups or by "portions." Thus, this is the majority of Dactylogyridae, Polystomatidae, Diclybothriidae, and many other fresh water and marine p. 91
species the eggs of which are without offshoots. On the other hand, here also is related the often-mentioned *Microcotyle gotoi* Yamaguti. According to

our observations the eggs of this species, numbering about 75 to 125, form a packet of very long filaments by means of entwining, which (the packet, nobis) is deposited all at once and does not delay itself on the gills of the host but falls into the water. In the water it turns upside down with the spool of the filaments down; the eggs comprising it spread fanwise in all directions forming a shape similar to that of a little umbrella or parachute which settles very slowly. The little feet of the eggs point in all directions with their hook-shaped ends and grab the sea plants and prevent the whole group of eggs from settling out of the water. This contrivance undoubtedly is consistent with the conditions of life of the Terpug, Hexagramidae--the host of M. gotoi--so that the emerging larvae will fall into more or less favorable conditions for the infection of the young host (for more details see page 118). As a rule the eggs of the representatives of the second group have more or less well-developed little feet and very often filaments. Often the eggs attach themselves to the body of the host by the little feet, and it is quite probable that they attach themselves not only mechanically by the terminal widening but also glue themselves to it. Usually during this process the maternal individual performs special motions while depositing the eggs which help in the gluing of each egg individually. Thus, the eggs of Nitzschia sturionis (Abildgaard), according to our observations, glue themselves to the mucous membrane of the buccal cavity of sturgeon-type fishes. Even in artificial conditions in a glass container the eggs glue themselves so strongly that they cannot be torn away by a strong stream of water from a pipette. Among species with sharpened feet and filaments, the latter retard themselves on the body of the host by mechanical action. For instance, according to our observations of Mazocraes of Caspian herring, during the period of intense egg-laying on the gills of the host there are many hundreds of deposited eggs and they are attached to the gills very strongly in spite of the fact that they do not have any special growths or indentations on the little feet or on the filaments. It is quite probable that the gluing of certain Hexabothriidae in long chains of from 10 to 15 units each, which was observed by Thaer (Thaer, 1850), appears as an adaptation to the easier retention of the eggs on the body of the host. There is reason to believe that the eggs of all monogenetic trematodes have an envelope which is agglutinous to some extent. Study under artificial conditions, however, does not permit us to substantiate this with complete conviction.

Embryological development of the egg-laying species has been insufficiently studied. For all practical purposes only the development of Polystoma integerrimum Froelich was studied (Goldschmidt 1902a, 1902b; Halkin, 1901).[1] In this species the cleavage is complete and unequal and at the same time irregular. Only in more advanced stages, the gradually larger blastomeres are grouped in the middle with the smaller ones around and an epibolic gastrula results. Then all the borders of the cells disappear and a syncytial mass results inside of which occurs isolation of the rudiments (anlage, *nobis*) of the tissue's and of the organs of the larvae. One must suppose also that among the remaining egg-laying monogenetic trematodes the embryological development takes place in a similar fashion and consequently the presence of a holoblastic egg of irregular cleavage and epibolic gastrulation is characteristic for this entire group. Among viviparous forms the cleavage was studied by Metschnikoff (Metschnikoff, 1870), Wagener (Wagener, 1860) and Kathariner (Kathariner, 1904). All these p. 92 authors worked on the development of different species of *Gyrodactylus.* Among the representatives of this genus the cleavage takes place just as irregularly and chaotically as among *Polystoma*. In the cleavage of the egg of *Gyrodactylus* it is characteristic that in the very early stages one large blastomere individualizes itself and later becomes the origin for the embryos (germ) of the following generation. As is known, a very peculiar development is observed among *Gyrodactylus* during which a number of larvae are formed from a single egg, not at the same time, but gradually one after the other. Gastrulation in *Gyrodactylus* is just as epibolic as in *Polystoma.* However, the formation of the syncytial mass does not take place and organogenesis develops by way of differentiation of cellular sections. The entire development unfolds inside the uterus of the maternal organism and an adult worm is born which does not differ in size from the maternal individual. A peculiarity of the development of *Gyrodactylus* is that during the very early stages, a second embryo forms inside the first embryo, inside of which soon is incepted a third and inside the last sometimes even a fourth. A number of researchers headed by Kathariner who worked specially on this question consider this phenomenon as polyembryonia, and others take it as one of the forms of paedogenesis. In order not to return again to *Gyrodactylus*, let us note that the development of the attaching apparatus among the representatives of this genus coincides in basic characters with that of Dactylogyridae (see development of *Dactylogyrus*, page 139).

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[1] P. G. Svetlov pointed out to us the existence of one more work (Minouchi, 1936) which was not known to us at the time of the writing of the present section.

The periods of the development of eggs from the moment of their deposition until the emergence of their free-swimming larvae are very different species and, as was shown by a number of studied, depend to a large degree upon the temperature of the surrounding medium. Generally one may say that in normal temperature conditions (obviously varying among the different species) the development lasts from 3 to 35 days; however, these periods can be considerably altered artifically; (for periods of development of the separate species see the "Appendix," pages 13 to 216). Thus, according to the data of Lyman (1951a), at the temperature of 4 degrees C the development of the eggs of *Dactylogyrus vastator* Nybelin does not take place at all. At a temperature of 8 degrees the larvae of *D. vastator* emerge from the shell of the egg on the 27th or 28th day, at 12 degrees --10th to 11th day, 16 degrees --6th to 7th day, 20 degrees --on the 5th day, 24 degrees --4th day, and 28 degrees --3rd day. In our opinion, these numbers are close to the truth but understandably err by excessive precision and definiteness. Actually, the process of development of larvae undoubtedly fluctuates considerably at the same temperature and conversely the period of development can be the same under fairly strong fluctuations of the temperature (Bychowsky, 1933). The larvae emerge from the eggs through an aperture which is formed on the upper end of the egg after the falling away of the operculum. The latter is opened due to the slight jars of the larva which is lying in the egg and sometimes only after considerable effort on its part, in a number of cases during the course of two to three hours. Very often, in normal conditions we happened to observe the deaths of larvae of the latter because of the impossibility of opening the egg due to the fact that it was overgrown by certain vegetable or bacterial organisms. As a rule, the little larva formed in the egg normally lies with the head end toward the operculum of the egg. In rare cases we observed the formation of little larvae lying the other way around, and these larvae in a majority of cases were unable to turn around and come out of the egg. The emergence of the larvae usually takes place during the warmer time of the twenty-four - hour period, predominantly in its first half, and with the lowering of temperature it is possible to retard the emergence of fully formed larvae for several days.

Undoubtedly the illumination of the latter exercises considerable influence on the emergence of the larvae from the eggs, thus it was possible for us to delay for rather long periods the emergence of the larvae among a number of species of Axine by placing the eggs in a dark place. And we were able to regulate the emergence of formed larvae precisely enough by switching them to a lighted place. p. 93

The larvae which emerge from the eggs move at first almost in straight lines, now accelerating, now delaying their motion. During the time of this first period of their life the larvae are characterized on the one hand by a strongly expressed positive phototropism; on the other hand by the inactive condition of the attaching apparatus because of which they cannot attach themselves to the body of their host. Both these peculiarities represent an important adaptation to the creation of the best conditions of dissemination of the larvae in the water. This period is succeeded after a certain interval by another, and is characterized by the fact that the larvae acquire ability for attachment and that among them the positive phototropism disappears or at least is strongly reduced and, for the most part, the negative phototropism is acquired. During this time, which is the longest in the larval period, the larva swims with undiminished speed but quickly changes

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[1] The negative phototropism of the larvae of Diplorchis ranae Ozaki indicated by Ozaki (Ozaki, 1935b) is undoubtedly related to the following (second, nobis) period of the life of the larvae.

its direction, often stopping and bumping against different objects as if feeling them with its anterior end and often attempts to attach itself by its posterior end. When it finds a host the larva passively or actively penetrates to its place of habitation, attaches itself and, casting away its ciliary coverings, begins its parasitic life. However, when it fails to find its host the larva does not perish at once but still swims for a long time although it already does not move its attaching disc and its armature, having lost the ability to attach.

In such a fashion,we can distinguish two periods in the normal life of the larvae with different physiological characteristics which can be distinguished morphologically at the same time by the condition of the attaching disc. During the first period, the latter carries its chitinous armature inside the body and only after it "cuts itself" outside and the sharp ends of the hooks penetrate or protrude and begin to move actively does the larva acquire the ability to attach itself to the body of the host. It is precisely the moment of the "emergence" of the hooks that determines the change of the larva from the first period to the second period. The time of the presence of the larvae in the first period varies. For the majority of Dactylogyrus it is equivalent to two to three minutes or even shorter, whereas for Nitzschia sturionis (Abildgaard)--not less than five minutes and in most cases longer (from 10 to 12 minutes). Then the second, most important period is considerably longer. Thus,for Dactylogyrus it is not less than 4 to 5 hours and for Nitzschia about 24 hours.

The biological significance of the two periods of life of the larva is very great. Actually the ability of the larva to swim actively is an adaptation for the dissemination of the species to different individuals of its host. If the larva had the ability to attach itself immediately to the body of its host the infestation of the individual of the parent host on which the egg was developed would have increased to a considerably greater degree than the infection of other individuals, which undoubtedly would not have been advantageous from the point of view of dissemination and consequently from the point of view of the flourishing and preservation of the species. The existence of the first period of life of the larvae appears to be a supplementary special adaptation which prevents increased infection of the same host individual. Indeed, both the increased activity of the larva and its positive phototropismplus its inability to attach--all these do not allow it to remain on the same host individual but force it to seek another. p. 94

The above-mentioned adaptations undoubtedly play a greater role among worms,the eggs of which remain on the host,than among those which deposit eggs on the bottom.

Postembryonic development of the egg-laying monogenetic trematodes has been studied somewhat better than the embryonic, but is also insufficiently known. Basically, at our disposal there are data about the structure of the newly emerged larvae and only to a small degree do we know about the nature of the further development up to the time of maturity. At the present time, literary data concerning the development of 13 genera and 22 species are known to us,[1] namely: 1) Acolpenteron catostomi Fischthal and Allison, 2) Dactylogyrus vastator Nybelin, 3) D. anchoratus (Dujardin), 4) D. crassus Kulwiec, 5) D. formosus, Kulwiec, 6) D. wegeneri Kulwiec, 7) D. macracanthus Wegener, 8) Ancylodiscoides vistulensis Siwak, 9) Benedenia melleni (MacCallum), 10) Polystoma integerrimum Froelich, 11) Polystoma nearcticum (Paul), 12) Polystomoides oris Paul, 13) Diplorchis ranae Ozaki, 14) D. scaphiopi Rodgers, 15) Sphyranura oligorchis Alvey, 16) Octostoma scombrii Beneden and Hesse, 17) Diclidophora luscae (Beneden and Hesse), 18) D. pollachii (Beneden and Hesse), 19) Diplozoon paradoxum Nordmann, 20) Microcotyle spinicirrus MacCallum, 21) M. donavini Beneden and Hesse, 22) Diplasiocotyle johnstoni Sanders.

From 1928 to the present time, 24 genera and 62 species were studied for the first time and checked for the verification of the data of previous researchers by us and by our collaborators.[2]

*1. Dactylogyrus vastator Nybelin
*2. D. anchoratus (Dujardin)
*3. D. solidus Achmerow
*4. D. formosus Kulwiec
*5. K. wegeneri Kulwiec
*6. D. intermedius Wegener
*7. D. cornu (Linstow)
*8. D. fallax Wegener
*9. D. crucifer Wagener
*10. D. longipula Bychowsky
*11. D. varicorhini Bychowsky
*12. D. pulcher Bychowsky
*13. D. modestus Bychowsky
14. D. curvicirrus Achmerow
15. D. gussevi Achmerow
16. D. phoxini Malewizkaja
17. D. erythroculteris Gussew
18. D. achmerowianus Gussew
19. D. obscurus Gussew
20. D. contortus Gussew
21. D. leucisculus Gussew
22. D. peltatus Gussew
*23. Dogielius planus Bychowsky
*24. Ancyrocephalus paradoxus Creplin
*25. A. (s. lat.) cruciatus (Wedl).
*26. A. (s. lat.) vanbenedeni (Parona and Perugia)
27. A. (s. lat.) pavlovskyi Gussew
28. A. (s. lat.) morgurndae Yamaguti
29. A. (s. lat.) curtus Gussew

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[1] References to authors who conducted experiments are reproduced in the appendix (pages 138 to 216). Data from the published works of our laboratory are not included in the present list.

[2] Those which were studied by us personally are noted by asterisks.

30. *A.* (*s. lat.*) *hemibarbi* Achmerow
*31. *Protancyrocephalus strelkowi* Bychowsky
*32. *Ancylodiscoides siluri* (Zandt)
*33. *A. vistulensis* (Siwak)
34. *A. varicus* Achmerow
35. *A. strelkowi* Achmerow
36. *Bychowskyella pseudobagri* Achmerow
*37. *Diplectanum aculeatum* Parona and Perugia
*38. *D. similis* Bychowsky
*39. *Heteroncholeidus buschkieli* Bychowsky
*40. *Lamellodiscus elegans* Bychowsky
*41. *L. fraternus* Bychowsky
*42. *Calceostomella inerme* (Parona and Perugia)
*43. *Tetraonchus monenteron* (Wagener)
*44. *Tetraonchoides paradoxus* Bychowsky
*45. *Nitzschia sturionis* (Abildgaard).
*46. *Benedenia derzhavini* (Lajman)
*47. *Polystoma integerrimum* Froelich
*48. *P. ozaki* Price
49. *Neopolystoma palpebrae* Strelkow
*50. *Diclybothrium armatum* Leuckart
*51. *Mazocraes alosae* Hermann
*52. *Octostoma scombri*, Beneden and Hesse
*53. *Diclidophora denticulata* (Olsson)
*54. *Discocotyle sagittata* (Leuckart)
*55. *Diplozoon paradoxum* Nordmann
*56. *Microcotyle mugilis* Vogt
57. *M. pomatomi* Goto
*58. *M. gotoi* Yamaguti
*59. *M. sebastis* Goto
60. *Axine belones* Abildgaard
*61. *Axine* sp. I
*62. *Axine* sp. II

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Altogether,in this fashion we dispose of the data about the development of 29 genera (75 species) related to the following 13 families: Dactylogyridae (Dactylogyrinae--Acolpenteron Fischthal and Allison, *Dactylogyrus* Diesing, *Dogielius* Bychowsky; Ancyrocephalinae--*Ancyrocephalus* Creplin, *Protancyrocephalus* Bychowsky, *Ancylodiscoides* Yamaguti, *Bychowskiella* Achmerow, *Heteronchocleidus* Bychowsky), Diplectanidae (*Diplectanum* Diesing, *Lamellodiscus* Johnston and Tiegs), Calceostomatidae (*Calceostomella* Beneden), Tetraonchidae (*Tetraonchus* Diesing), Tetraonchoididae (*Tetraonchoides* Bychowsky), Capsalidae (Benedeniinae--*Benedenia* Diesing, Nitzschiinae *Nitzschia* Baer), Polystomatidae (*Polystoma*) Zeder, *Polystomoides* Ward, *Neopolystoma* Price, *Diplorchis* Ozaki), Sphyranuridae (*Sphyranura* Wright and MacCallum), Diclybothridae (*Diclybothrium* Leuckart), Mazocraeidae (*Mazocraes* Hermann, *Octostoma* Otto) Diclidophoridae (*Diclidophora* Diesing), Discocotylidae (*Discocotyle* Diesing, *Diplozoon* Nordmann), Microcotylidae (*Microcotyle* Beneden and Hesse, *Axine* Abildgaard, *Diplasiocotyle* Sanders).

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Fifteen families remain unstudied--Protogyrodactylidae, Monocotylidae, Loimoidae, Dionchidae, Microbothriidae, Acanthocotylidae, Amphibdellatidae, Bothitrematidae, Hexabothriidae, Chimaericolidae, Hexostomatidae, Anthocotylidae, Plectanocotylidae, Protomicrocotylidae, and Gastrocotylidae.

The study of representatives of these families is a problem of first priority and above all Microbothriidae, Bothitrematidae, Hexabothriidae and Hexostomatidae should be studied because their location in the system is doubtful and information about larval stages must play a deciding role in the final elucidation of this question.

Because the number of unstudied families is larger than those studied,it appears at first sight that it is premature to make generalizing conclusions; however, this is not true, inasmuch as we can also judge the structure of the larvae in the majority of the unstudied families from the existing data. We cannot expect principal differences among the larvae of Protogyrodactylidae and Dactylogyridae,and (judging by, nobis) the structure of the adults we can say with great accuracy what the larvae must be in this aberrant family. The same can be said about Monocotylidae, Loimoidae and Dionchidae, the larvae of which must be very close to those of Capsalidae. The structure of the larvae of Acanthocotylidae is clear, because the adult individuals have an unchanged larval disc. The larvae of Amphibdellatidae and Tetraonchidae are undoubtedly very close. There are no special doubts, either about the larvae of Anthocotylidae, Plectanocotylidae, Protomicrocotylidae, or Gastrocotylidae because the structure of the adult individuals provides the basis for a sufficiently precise idea about the nature of their larvae. In such a fashion the material which exists on the subject of the development of the 13 families gives fully sufficient data for the general representation about the larval stages of the overwhelming majority of Monogenoidea. It is understandable that separate details of the structure p. 96 remain unknown, but this concerns mainly the secondary peculiarities from the point of view of the analysis of the phylogeny of the group.

All the data on the subject of the development of separate species are placed by us into a separate appendix (pages 138 to 216) to which we refer those who are interested. Here is expressed only generalized material about the character and peculiarities of the postembryonic period and the development of monogenetic trematodes.

The presence of the free-swimming larva equipped with a ciliated covering is characteristic for all Monogenoidea. Representatives of Gyrodactylidae appear as exceptions, inasmuch as they are viviparous. We consider the data of Alvey (Alvey, 1936) about the absence of the ciliated coverings among free-swimming larvae of Sphyranura oligorchis Alvey as erroneous (see page 192).

Basically the larvae of all monogenetic trematodes are characterized by the following signs: first, the presence of a ciliated covering, located mainly in three zones--near the head end, in the middle of the body, and near the attaching disc; second, by the presence of head glands the efferent ducts of which are grouped by bunches opening outside in the anterior head lobe of the body; third, the presence of strongly differentiated systems of internal organs--of the digestive system with the pharynx and intestine developed to a certain degree, with the excretory system with basic ducts and a number of protonephridial cells and a nervous system with isolated head ganglia and longitudinal nerve trunks and one to two or four eyes (a number of exceptions); fourth, powerfully developed attaching discs always equipped with chitinous armature consisting of a certain number of varying or similar hooks.

One can expect that the enumerated characters probably were also characteristic for the primary larvae of monogenetic trematodes and it appears to us that in addition, one should consider the location of the buccal aperture on the ventral surface much closer to the middle of the length of the body than is observed among contemporary species, as very probable, for we see that the buccal operture is located closer to the midole of the body among larvae of more primitive contemporary Monogenoidea than among the more highly organized ones. The nature of the ciliary covering of contemporary species does not allow us to speak with certainty concerning the direction of its evolution, but nevertheless it is probable that initial forms possessed a continuous ciliary covering and its division into separate zones is a secondary phenomenon. Further, it is completely clear that hooks were the initial armature of the ancestors of monogenetic trematodes and not suckers or clamps which, just as in the individual development, historically appeared later. In all probability among the ancestral species the chitinous armature of the attaching disc was represented by a great number of hooks equal in form and size and lying along the edges of the posterior end of the body which was not yet differentiated into the form of a disc (which was, nobis) apparently already somewhat flattened, as we observe among a number of Rhabdocoela. A clearly expressed tendency toward the decrease in the number of edge hooks in proportion to their morphological complication among contemporary monogenetic trematodes serves as a basis for these suppositions. Such a larva (Fig. 114) of monogenetic trematodes does not differ in principal from the adult form which develops from it. Basically the differences can be reduced to the appearance and development of the sex system and the progressive growth of the organs of all systems. Concerning the sex system, we can maintain that it was incepted p. 97 and developed in the posterior half of the body behind the end of the intestinal system. Finally, it is not less probable that the ciliary covering of the larvae remained during their attachment to the host in the beginning as this happens in a number of ectoparasitic Turbellaria. Having thus recreated in considerable measure a promonogenetic trematode (Fig. 115), we see that its similarity with the Turbellaria is so great that we could, without any hesitation place such a form in the same group as Rhabdocoela, which agrees with the commonly accepted view of the origin of monogenetic trematodes. The development of the chitinous armament of the posterior end of the body, which assume the function of attachment at the expense of a decrease in the role of the adhesive glands attaching to the substratum, which are so characteristic of Turbellaria, can, by themselves, serve as the basic character indicating the formation of the new group.

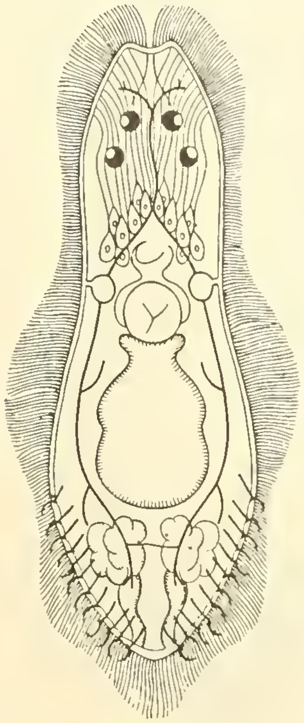

Fig. 114. Hypothetical free-swimming larva of promonogenetic trematodes. Explanation in text.

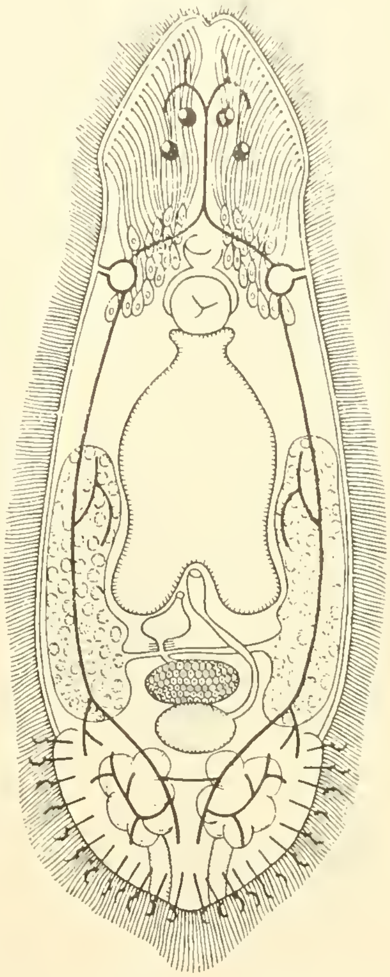

Fig. 115. Hypothetical promonogenetic trematodes. Explanation in text.

We can clearly divide the larvae of monogenetic trematodes into two basic groups differing by a number of characters and at the same time characteristic for two morphologically different groups of adult Monogenoidea. To the first group are related the larvae of eight families–Dactylogyridae, Diplectanidae, Calceostomatidae, Tetraonchidae, Tetraonchoididae, Capsalidae, Polystomatidae, Sphyranuridae. And to the second,the remaining five --Mazocraeidae, Diclidophoridae, Discocotylidae, Microcotylidae, and Diclybothriidae, The last family, however, has a number of distinctive traits which place it somewhat in isolation (see further page 404).

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A typical larva of the first group has the following structure (Fig. 116). Its body is elongated and cigar-shaped, and it is provided with three zones of ciliary epithelium. There are well-developed head glands which open outside by two groups of ducts on the anterior edge of the head end. The anterior end of the body has two pairs of well-developed pigmented little eyes with light refracting lenses. The buccal aperture is located ventrally at the level of the first pair of eyes or even in front of it. The pharynx is powerfully developed, the intestine is circular. There is a weakly developed nervous system and excretory system. The sex system is not developed but for the most part a group of large cells representing p. 99

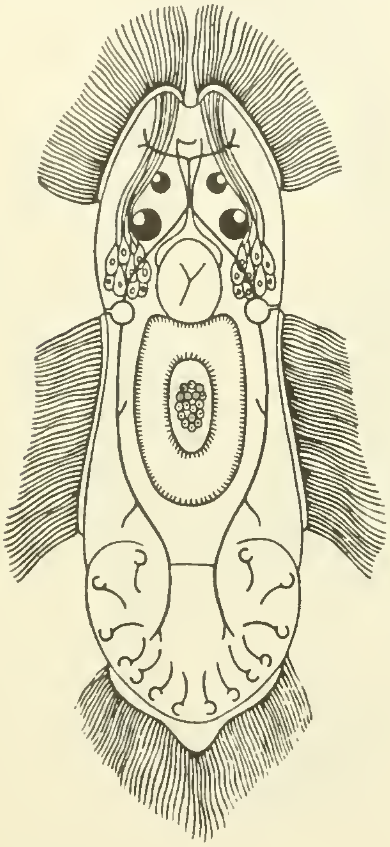

Fig. 116. Free-swimming larva of the first type. Explanation in text.

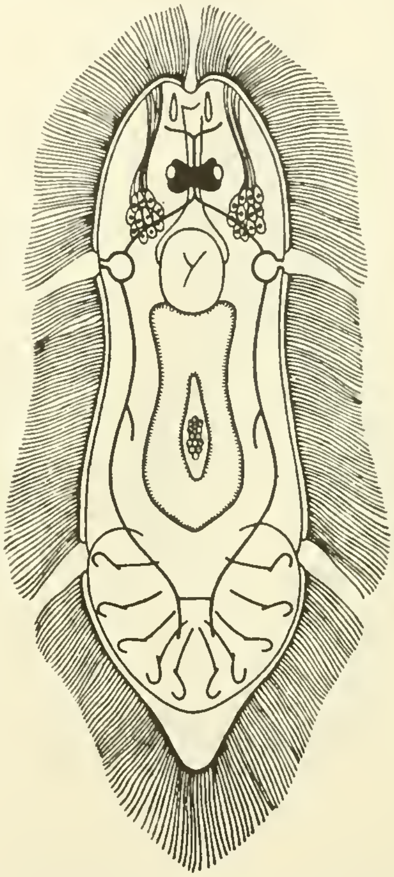

Fig. 117. Free-swimming larva of the first type. Explanation in text.

the sex embryo (gonad anlage, nobis) lies inward from the intestinal ring. The attaching structure of the posterior end of the body consists of 14 to 16 edge hooks. They have a well-developed terminal little hook and a more or less well-developed handle. The latter is firm, hard and not flexible. Its growth (if it takes place in the postembryonic period) takes place at the expense of a super growth (accretion, nobis) at the free end (skeleton-forming cells lie near the upper end of the handle.)

The larvae of the second group (Fig. 117) have a similar body shape and are also equipped with a ciliary covering which is divided into three zones, but which for the most part is more powerfully developed. There are also well-developed glands of the head end opening outside for the most part by three groups of ducts. Usually, the eyes are in the number of one fused from two (which is clearly indicated by the presence of two light refracting lenses), more seldom there are two eyes and even more seldom--four (Diclybothrium, Axine). The buccal opening is somewhat closer to the anterior end than among the larvae of the first type. The pharynx is powerfully developed and is located at a greater distance from the buccal opening, the intestines are circular or sac-shaped. A development of the nervous system and excretory system is approximately the same as in the first group. The sex system is incepted behind the intestinal sac or in the same fashion as among the larvae of the first group. The attaching armature of the disc consists of ten to twelve edge hooks or, as an exception, of a smaller number (genus Diplasiocotyle), or the edge hooks can even be absent, but then there are other attaching formations (genus Diplozoon). As a rule the edge hooks of this group are already fully developed during the period of embryonic development and differ from the edge hooks of the larvae of the first group in that their little hook is more elongated, whereas the handle is straight or slightly curved, more delicate and flexible.

Within the limits of the group of the larvae of the first type we observe differences in the attaching apparatus which have quite regular character. On the one hand, they concern the chitinous armature of the disc, and on the other hand, the appearance of attaching formations supplementary to it--suckers. As was pointed out earlier for the families of Monogenoidea which have similar larvae, the attachment of adult forms takes place either only with the help of chitinous armature or with the help of the disc--sucker, or with the help of suckers on the attaching disc. It is understood that between these methods of attachment there are a number of transitions when the worms attach utilizing different formations at the same time. The most primitive undoubtedly appears to be the attachment with the help of the chitinous armature (alone, nobis) and the most complex for a given group--suckers. The change in the structure of the attaching apparatus of the larvae develops in the same direction as the adaptation to the attachment among adult forms. The larvae of Dactylogyridae, Diplectanidae, and Tetraonchidae possess only chitinous armature, and the adult forms of this family also attach only with its help. The larvae of Calceostomatidae and Capsalidae possess only chitinous armature also, but their adult forms maintain themselves on the host mainly by means of a disc transformed into a sucker. Tetraonchidae and Tetraonchoididae, which have a larva similar to the more simply organized Dactylogyridae, probably attach themselves with the help of a disc and partially by chitinous armature. The larvae of Sphyranuridae attach themselves with the help of chitinous hooks and suckers in the same fashion as their adult forms. Finally, in the adult condition, Polystomatidae attach themselves only by suckers, whereas the larvae have only the chitinous armature. At first glance there appears almost no correlation in the p. 100 structure of the attaching apparatus of the larvae and in the adults; however, it is far from that. The edge hooks of the larva which have just emerged from the eggs of the more simply organized monogenetic trematodes have not yet reached their final sizes and shapes, whereas among highly organized representatives they acquire their permanent sizes and shapes in the embryonic period. Similarly, we observe that edge hooks of the first (group, nobis) reach relatively larger sizes than those of the second. At the same time with this, the lowly organized forms have a more complexly arranged handle of the edge hooks which among them is often differentiated into a number of divisions well-delineated from each other. Finally, very often separate pairs of edge hooks are distinguished from each other by size which happens only in exceptional cases among highly organized monogenetic trematodes of this group.

Along with the changes of edge hooks, we observe the appearance of middle hooks, which also have a regular character. Among the more lowly organized groups they are absent from the free-swimming larvae and also among adult forms (the absence of middle hooks appears as a secondary phenomenon among highly organized species). Later, middle hooks appear, at first--after the embryonic period, and then during it in such a way that the inception of the hooks takes place successively during more or less early stages, and finally - entirely in the egg. The free-swimming larvae grow a successive number of middle hooks from one pair to three as is the case among adult forms. Just as in the edge hooks, one can note that the relative tempo of the growth of the middle hooks decreases with the increase in the organization of the adult animal.

Finally among those species which have been studied, the larva of Sphyranura oligorchis already has one pair of suckers in addition to the chitinous armature as it emerges from the egg, just as the adult form. The growth of the middle hooks and suckers of Sphyranura continues even later.

The second group of larvae demonstrates basically the same normal complications of the attaching apparatus. Among the adult animals related to it, attachment by means of clamps or the presence of sucker-shaped clamps is characteristic, as among Diclybothriidae and Diclidophoridae. Their number varies greatly within limits of the entire group, but the general tendency goes toward the increase of their number from four pairs to several tens or even hundreds. The larvae emerging from the egg have chitinous armature of the hook type and some more highly organized forms also have clamps. Among Mazocraeidae and Diclidophoridae, the free-swimming larvae have five pairs of edge hooks, Discocotylidae have three pairs of edge hooks (among Diplozoon paradoxum they are absent), one pair of middle hooks and one pair of attaching clamps. Microcotylidae usually have five pairs of edge hooks and two pairs of middle hooks [among Microcotyle spinicirrus MacCallum, six (?) pairs of edge hooks and among *Diplasiocotyle johnstoni* Sand. three pairs of edge hooks and finally *Microcotyle mugilis* Vogt has, besides edge and middle hooks, still one more pair of attaching clamps] , Diclybothriidae, five pairs of edge hooks and two pairs of middle hooks. For representatives of these groups it is characteristic that all hooks, the lateral as well as the middle, do not grow at all during the postembryonic period. As a rule they are either retained unchanged during the entire life or are replaced by a clamp or are even discarded from the body of the animal (see page 212). The exception is represented by Mazocraeidae among which, during the postembryonic period, there appears still one more pair of middle hooks which (and only p. 101 they) grow for a sufficiently long period and considerably, and Diclybothriidae among which the relationships are somewhat more complicated (see further). Within the limits of this group we see certain tendencies toward the decrease in the number of edge hooks among specialized species (*Discocotyle*, *Diplozoon*, *Dipliasiocotyle*). Finally it is extremely curious that the attaching clamps of the first four pairs are incepted on the bases of the edge hooks, which apparently enter into the composition of the chitinous parts of the clamps to some degree. Among monogenetic trematodes which have more than four pairs of clamps, all incepted after the first eight are formed without the participation of edge hooks, and by this they differ principally from the preceding ones. V. A. Dogiel (1954) writes on the subject: "From here we can make the following essential conclusion: in the first place all the anterior clamps of Microcotylidae have a different origin than the four posterior(pairs, --B. B.) and because of that are not homologous to them: in the second place, because of what has just been mentioned, the formation of numerous anterior clamps must be considered not as polymerization (that is the multiplication of a number of homologous organs) but as a numerous (plural, *nobis*) inception of new organs not homologous to the posterior -- four (pairs, -- B.B.) clamps." Subsequently, the clamps of the larvae which have relatively very small sizes grow considerably. Their growth differs significantly from the growth of the hooks because all the parts of the clamps are incepted at once, but in small sizes, and after that they grow equally in all their parts.

A few words about middle hooks in the larvae of this group. Middle hooks of the larvae of Mazocraeidae, Discocotylidae, Diclidophoridae, and the first pair of middle hooks of the larvae of Microcotylidae generally strongly resemble the edge hooks in their shapes and differ mainly in their somewhat larger sizes. It seems to us that, taking into consideration their appearance in the embryonic period at the same time with the edge hooks and also the places of their inception, it is more correct to consider them as the sixth (more precisely the first) pair of edge hooks; whereas the second pair of middle hooks, which is incepted in the embryonic period among Microcotylidae and in the postembryonic period among Mazocraeidae, clearly differs in structure and is not equivalent to edge hooks.

As was already indicated, the larva of Diclybothriidae (Fig. 221) appears somewhat different from the other larvae of this group; it has, in addition to the typical five pairs of edge hooks, two pairs of middle hooks and the latter are of strange shape not resembling any of the middle hooks of other species which have been studied. In our common work with A. V. Gussew (Bychowsky and Gussew, 1950) we wrote: "Homology of the chitinous hooks of the larvae with the ones of the adult animals does not occasion any doubt. The anterior three pairs of edge hooks correspond to the hooks of the suckers--clamps, the fourth pair--to the third pair of hooks of the narrowed part of the disc, the fifth pair corresponds to the small hooks of the posterior end and in this fashion it is the only one of them all which is not subjected to any noticeable change in sizes and form. The first and second pairs of middle hooks of the larvae correspond to the ones of the narrowed part of the disc of the adult individual. It is curious to note that the latter hooks and the second pair of middle hooks of the larvae, which strongly differ in shape acquire considerable similarity during further development. One must note this circumstance in light of the evaluation of the interrelationships of the chitinous formations of the adult individuals for the building of phylogenetic links within the limits of the group." From what has been said, one must consider that in comparing the chitinous armature of Diclybothriidae with the one of Microcotylidae, the first pair of middle hooks p. 102 of the latter corresponds to the second pair of the former and conversely the second pair, that is actually the middle hooks of Microcotylidae, correspond to the first pair of the hooks of Diclybothriidae.

At first glance the presence of two pairs of pigmented eyes, which are not observed among all other larvae of the second type, appears to be a basic difference between the larvae of Diclybothrium and the other larvae of this second group as well as the majority of the larvae of the first type. However, we have often indicated that within the limits of the most diversified group of Monogenoidea there exists a tendency toward the reduction of (the size of, nobis) eyes and of their number. Taking into consideration also that within the limits of one family eyes can be either present or absent among closely related types, this circumstance cannot have serious phylogenetic significance. This is substantiated by the very convincing data on the embryology of Axine which appears to be a typical Oligonchoinea. The larvae of this genus which were examined have four eyes and it is essential that among Axine sp. I both pairs are normally developed, among Axine sp. II the anterior pair fuses and the second is normally developed and relatively larger whereas, among A. belones Abildgaard, the anterior pair is fused while the posterior is very weakly expressed. There is clearly a tendency toward the disappearance of the second pair of eyes and the preservation of one fused eye, which is characteristic for typical Oligonchoinea (see page 214).

In such a way, returning to Diclybothriidae, it seems clear that their larvae belong in the category of the second type despite some differences, just as the family itself stands within the limits of Oligonchoinea (see page 402). As a peculiarity of the family connected with the morphology of the adult forms appears the fact that, as has been pointed out, all chitinous elements, with the exception of the fifth pair of edge hooks, grow intensely during the first embryonic period. Apparently the family of Hexabothriidae (see page 405), which was studied by us, has the same peculiarities.

The subsequent development of the larvae of both types proceeds with a varying degree of speed according to the degree of complication of the attaching apparatus, on the one hand, and of the progressive development of all systems of internal organs on the other hand. The complication of the attaching apparatus from the larval stage to the one possessed by the adult forms is observed in the following directions: 1) intensified development of the chitinous attaching apparatus of the hook type; 2) intensified development of the attaching disc itself as an organ of attachment; 3) the development of the suckers or attaching clamps on the attaching disc in the process of development; 4) the appearance of new disc-shaped organs of attachment not homologous to the initial (or primary, nobis) attaching disc.

The development of the hooked chitinous apparatus proceeds along the line of complication and differentiation of edge and middle hooks and the appearance of supplementary chitinous formations supporting the hook apparatus and coordinating its work. The edge hooks of the more primitive Monogenoidea have the same shapes in all stages of life and grow synchronously with constant speed. Among more highly-organized species the process develops along two lines--on the one hand deviation in sizes of different pairs of edge hooks often accompanied by a change in shape takes place, and on the other hand the changes proceed along the line of preservation of the initial sizes of the hooks and a gradual loss of their significance with the increasing role of the middle hooks. The latter have, as was indicated earlier, varying shapes and sizes and a tendency toward the p. 103 increase of the number from one to two or even three pairs. In connection with the complication in the structure of the hooks and their more powerful development, connecting plates of different types which were already mentioned (see page 28) usually appear. As a rule, these connecting plates are developed more powerfully in forms having a larger disc and more powerful armature. In an original form of Heteronchocleidus buschkieli Bychowsky (see page 164 and Fig. 118) the adult worms have three powerfully developed middle hooks, the fourth remains undeveloped and the two connecting plates which appear are located in such a way as to serve for the connection of all three hooks into one coordinate system. Among many Diplectaninae the three connecting plates (Fig. 56) lie in such a way that on the one hand they support the disc in the completely unfolded shape, and on the other hand, they are connected with the four middle hooks so that the latter, lying in pairs, play the role of two attached, pincer-shaped systems and not four independent formations.

In a number of groups the role of the chitinous hook armature decreases in proportion to the growth of the animals and the powerfully developed disc acquires the main significance. It transforms into a sucker similar to that of leeches or digenetic trematodes. During this process the edge hooks do not grow as a rule but retain their initial sizes while the middle hooks remain without change, losing their signficance (Calceostomatidae), or continue to grow, partially preserving the attaching role and become mainly a supporting apparatus (Nitzschiinae and others).

Characteristic for Polystomatidae is the fact that the chitinous armature is preserved during the appearance in the postembryonic period of suckers on the attaching disc (the latter also increases strongly,[1] and the middle hooks grow and for a certain time still function, whereas the edge hooks remain partially on the posterior and anterior edges of the disc and partially in the centers of the developing suckers (one in each sucker) without changing sizes, but cease to function completely,

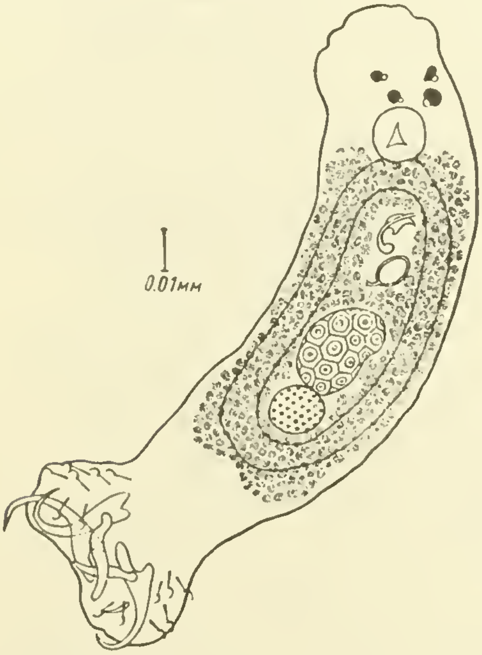

Fig. 118. Heteronchocleidus buschkieli Bychowsky, adult worm from the gills of little aquarium fish Macropodus opercularis (L.) Leningrad.

Among species in which attaching clamps develop in the disc, the fate of the chitinous larval armature differs, but generally it doesn't grow (exception, Diclybothriidae, see above) and is not fully preserved. For the most part the edge hooks enter into the composition of the clamps which are in the process of formation p. 104 and thus they disappear and one pair is either preserved for the entire life of the worms without change or is cast off completely. One pair of middle hooks that apparently represents modified edge hooks with changed shapes, as a rule does not grow (just as for edge hooks the exception is Diclybothriidae), whereas in a number of cases the second pair grows (Mazocraeidae) and in others remains without changes (Microcotylidae). In a number of Microcotylidae both pairs of middle hooks and one pair of the edge hooks, which was already indicated, usually lie in common in a small narrowed section of the posterior end of the attaching disc and they fall off during the early stages of postembryonic development together with this portion of the body.

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[1] Cases of its disappearance, although it may be partial, are known.

Finally, during the period of postembryonic development, certain species (*Diplectanum*) form special disc-shaped growths on the ventral and dorsal sides of the anterior part of the attaching disc and these growths are equipped with chitinous stick-shaped plates or chitinous rings which serve as auxiliary organs of attachment. Analogously to this, apparently, a secondary attaching disc is formed in Acanthocotylidae among which the primary disc loses its attaching signficance soon after the emergence of the larva from the egg, although it is preserved during the entire life of the worms.

During the time of the postembryonic period the development of internal organs takes place with different speed among various types, and what is most interesting is that very often the individual in the process of development, which has not yet reached its final form and in which a number of parts of the attaching apparatus are still undeveloped, already begins to produce eggs which are fully capable of further development. This is observed especially frequently among representatives of the genus *Dactylogyrus*. Interesting contrary data on postembryonic development of *Dactylogyrus vastator* Nybelin were obtained by N. A. Izumova. According to her materials, a fully developed copulatory apparatus appears after 3 to 5 days in the larvae which settle on the gills of the host (and at the same time also the attaching armature of the disc appears to be fully formed). However, the sex system of *D. vastator* is fully formed only on approximately the tenth day, and from that time the worms begin to produce eggs. Izumova succeeded in showing that the temperature of the surrounding medium has great influence on the development of the sex system and also on the attaching armature. Thus the larvae, the development of which took place in a temperature of 12 to 15 degrees, showed gradual change into the mature state. The copulatory organ and attaching armatures reached full development only in the fifth and sixth day. At a temperature of 18 to 22 degrees the character of the development of chitinous elements differed considerably. Thus, separate elements of the attaching armature were completely formed much earlier-- 2 to 3 days; just as the copulatory apparatus was formed at this period although, just as during the development under lower temperatures, the mature stage occurred not earlier than 7 days and in this fashion the process of spermatogenesis and oogenesis fell behind the development of chitinous parts.

In conclusion one must note, however, that there are almost no observations in our materials nor in the literature concerning the periods of postembryonic development, which understandably exceedingly complicates the comparison of existing data. Separate information on this question is given by us in the "Appendix" (page 138).

CHAPTER IV

LIFE CYCLES OF MONOGENETIC TREMATODES

Studies of the life cycles of parasitic animals are of great interest from the practical as well as the theoretical point of view. A precise knowledge of the life cycles gives into the hands of the specialists who are conducting a struggle with parasitic diseases the possibility of active interference with the course of the cycle during the periods which are susceptible to human countermeasures so as to disrupt the further normal course of life of the parasite and by this very action to eliminate any parasitic infection. The works on preservation of man from infection by *Dracunculus medinensis* in Central Asia serve as an outstanding example of this. p. 105

The theoretical significance of the study of the life cycles is not less important. Their knowledge opens the way to the origin and the processes of the establishment of parasitism and gives us understanding of the reasons for the nature of various parasites and also shows the role of historical factors in the function of interrelations between the parasite and the host. On the basis of the analysis of the life cycle of the parasite, we can ascertain the degree of the inherited fixation in its relations with the host, the role of factors of the external medium in relation to the parasite and the host, and the role of the host as an element of the medium of the parasite. All this taken together provides considerable material for the understanding of the evolutionary processes and thus is of general biological significance.

Before speaking about life cycles of monogenetic trematodes, we must also indicate what meaning we attach to this definition. A life cycle is a very complex phenomenon. It should not be considered apart from the relations between the animals and the medium in a simplified manner, as is customarily done when it denotes a period (extending, *nobis*) from the deposition of the egg by the maternal individual to the formation of the egg by the filial individual or that offspring which is equivalent to the maternal (stage, *nobis*) which is formed after a certain number of intermediate morphologically or ecologically distinctive phases. Into the understanding of the life cycles, in our opinion, must enter all phenomena which take place in the complex parasite-host-surrounding medium, from the formation of the egg of the maternal individual until the death of the progeny from this egg, including all stages of development of the daughter individual as well as the generations issuing from her but not equivalent to her morphologically. Within the life cycle, understood in this fashion, we differentiate the sex cycle connected with the reproduction and limited by the time from one period of reproduction to the other, the yearly cycle in which enter all the processes which take place during the year, and the cycle of development which comprises the above-mentioned period extending from the deposition of eggs until the formation of the individual which is equivalent to the maternal one.

The life cycles of monogenetic trematodes have been almost unstudied. There are data concerning the life cycles and the sex cycles of several representatives of the genus *Dactylogyrus* in the literature (Nybelin, 1925; Wilde, 1937; Gröben, 1940; Lyman, 1951b; Bauer, p. 106 1954; and others), *Polystoma integerrimum* (Zeller, 1872a, 1876; Gallien, 1934c, 1935), *Diplozoon paradoxum* (Zeller, 1872b), *Benedenia melleni* (Jahn and Kuhn, 1932), *Microcotyle spinicirrus* (Remley, 1942) and certain others (see chapter on development and the appendix thereto, pages 138 to 216). Along with these materials, which are far from complete, data about separate phases of the life cycles of various fresh water and marine Monogenoidea are scattered in numerous systematic works. Thus, this important question has not been subjected to serious specialized research until the present time. Our material is not exhaustive either, but nevertheless it furnishes a great deal (of information, *nobis*) for the understanding of the life cycles of monogenetic trematodes and contradicts the usual notions concerning their extreme simplicity.

When it becomes necessary to examine fishes on monogenetic trematodes (sic) of any body of water (when it becomes necessary to examine the monogenetic trematodes of fishes from any body of water *nobis*), especially marine, many instances provoke perplexity. First of all, in an overwhelming majority of the cases we find that only adult parasites, predominantly of the same age group, are encountered on these fishes, whereas different stages in development and the young worms either are encountered not at all or extremely rarely. Furthermore, what seems incomprehensible is the fact, as was mentioned earlier (see page 78), that very frequently the worms are encountered in 100 per cent of the cases in one age category of the host, but are absent in other (age categories of the same host, *nobis*). Still greater perplexity results from questions which arise from the study of certain pelagic fishes, as for instance the mackerel of the Black Sea. The eggs of monogenetic trematodes which parasitize this fish are deposited on the bottom. If one considers the conditions (of the bottom, *nobis*) of the Black Sea, one wonders how fishes can be infected 100 per cent when the hydrogen sulfide zone prevents eggs which fall to the bottom from developing. All these phenomena and many others which appear during the study of the distribution of monogenetic trematodes in nature are clearly a reflection of the peculiarities of the life cycles and not a chance or accident connected with the shortcomings of the research.

To have a correct approach to the understanding of the life cycle of monogenetic trematodes one must, first of all, clearly understand some of the biological groups. As has already been pointed out, Monogenoidea can be divided into two groups according to the method of reproduction, that is into a relatively small group of viviparous (only representatives of Gyrodactylidae) and another group of egg-laying types to which the overwhelming majority of species are related. This division points, also, at the same time, to a considerable difference in the method of infection of the host because the viviparous forms infect by means of direct contact with a host when they are adult worms, whereas the egg-laying forms infect, in the free-swimming larval phase, through the medium which surrounds the host. In their turn, as was described before, egg-laying forms fall into two groups--egg-laying proper, that is depositing eggs into the body of water in which the host and parasite are located, and into the egg-attaching group in which the eggs delay themselves for development on the body of the host. Evaluating what has been said above we can say that the deposition of eggs on the bottom appears to be more primitive, whereas the viviparous type with infection of the fish by means of contact appears to be more complex and undoubtedly is the latest historical development.

The simplest life cycle is of the form with a prolonged period of egg deposition in which eggs are deposited on the bottom of the water reservoir and with a free-swimming larva which has the ability of infecting the p. 107
host in all, or more precisely, in almost all phases of its (the host's *nobis*) life cycle. Such a type of life-cycle we observe among fresh-water representatives of the genus *Dactylogyrus.* The most studied is the cycle of an important parasite, *D. vastator* Nybelin. Because of the fact that a dissertation and a number of special works of N. A. Izumova (1953, 1956a, 1956b) are dedicated to the biology of this species, we shall dwell on the oviparous cycle only briefly.

The worms deposit eggs which develop in different periods depending upon the temperatures of the water. A number of authors (Nybelin, 1925; Nordquist, 1925; Wunder, 1929, and others) maintain that *D. vastator* has two types of eggs--"summer", relatively small and developing quickly and "winter", large and developing slowly. According to Nybelin, during the warm months reproduction takes place only by means of "summer" eggs and during this period a number of generations of the worms take place. Then, with the arrival of low temperatures, the worms begin to deposit large "winter" eggs which hibernate at the bottom of the body of water and terminate their development toward the following summer. The worms themselves all perish in the fall and are absent during the winter. Both questions, i.e., concerning "winter" and "summer" eggs and about the existence of adults during the winter time, appear to be fairly complicated and were solved only in recent times, and mainly by the work of the Soviet researchers. During the study of the periods of the development of the eggs of *D. vastator*, we established (Bychowsky, 1933d) that at a temperature of 21.5 to 24.5° the larvae will emerge from the egg on the fourth day, at a temperature of 18.2° on the fifth day, temperature 17.7°--in six days, temperature 16.4°--the seventh day, and somewhat later we observed that at a temperature of 15.5° the development continues for more than ten days. According to E. M. Lyman (1951a) who especially studied this question, at mean temperatures of 28° the development continues three days and at temperatures of 24°--four days, of 20°--five days, 16°--six to seven days, 12°--ten to eleven days, 8°--27 to 28 days, 4°--is totally absent. In such a fashion, a severe lowering of temperature not only retards development but also

interrupts it for a more or less prolonged period. As regards morphological differences between the "winter" and "summer" eggs one should consider them as nonexistent, or more precisely that the observed facts were not correctly interpreted. According to our observations and also according to the data of Kulwiec (Kulwiec, 1929), the same specimen of *D. vastator* deposits, at any time, eggs which vary extremely in size so that some could be considered as "summer" and some as "winter." However, their further development is completely uniform and no difference is observed in periods of development. It is clear from these reproduced data that in the spring infection can take place from hibernating eggs, but there is no basis for acceptance of the hypothesis of "winter" eggs to explain this. The existence of adult individuals in the winter periods, which is denied by a number of authors, is actually indisputable. Thus, as early as 1929 during our student work on the trematodes of the fishes of the Volga River in the vicinity of Kostroma, we succeeded in showing that all the species of *Dactylogyrus* occur in the coldest months of winter on the most diversified fishes. An unusually low quantity of parasites and also a severe lowering of the percentage of infection of separate fishes constitutes a peculiarity of winter infection. All subsequent studies substantiated the given conditions. Thus, A. P. Markevich found *Dactylogyrus* and even their eggs in January and February on the gills of Carp in the Nikolsk fish farm (Markevich, 1934). In the work of E. M. Lyman (1951b) are reproduced data concerning the infection of Carp during the winter by gill trematodes *D. vastator* and *D. anchoratus* (Dujardin) in which it is clear that for *D. anchoratus* the percentage of infection remains very high during the entire p. 108
winter, whereas for *D. vastator* both the percentage of infection and the quantity of the parasites are lowered. From the work of Lyman it is also apparent that he also observed egg-laying by *D. vastator* during the winter. This appears to us erroneous. It is more probable that Lyman dealt with individuals which began depositing eggs after the transfer of infected fishes into the laboratory, that is during the changed temperature regime.

Under natural conditions, the life span of *D. vastator*, as has been pointed out in Chapter 2, fluctuates very much, but in summertime it is not less than 20 to 25 days in spite of the opinion of Groben (Groben, 1940), who believes that *D. vastator* lives only 10 to 12 days (including the embryonic development). The individuals infecting fish in the late autumnal period partly perish during the lowering of temperature and partly hibernate. In such a fashion the life span of the latter can reach 6 7 months. The life of the separate individual from the moment of emergence of the larva from the egg consists of several hours of existence in the free-swimming stage and then a period extending from the moment of the settling of the larva on the gills of the host until maturity, a period which among *D. vastator* under conditions of the Leningrad region, i.e., at summer water temperatures about 14 to 17°, continues for 6 to 8 days, and the interval of time from the beginning of maturity until death, which extends not less than 12 days. The deposition of eggs takes place during the entire life of the worms but not with the same intensity (Fig. 119) depending upon external conditions, mainly on the temperature and oxygen regime. Data of N. A. Izumova (see page 86) show that under average conditions in the Leningrad region during the summer, *D. vastator* deposits from 4 to 10 eggs in the space of 24 hours. She also noted that under unfavorable conditions during the rising temperature and a worsening of oxygen regime the number of eggs deposited increases considerably. The observations of Izumova were conducted on worms which were located in natural conditions on the gills of their host.[1]

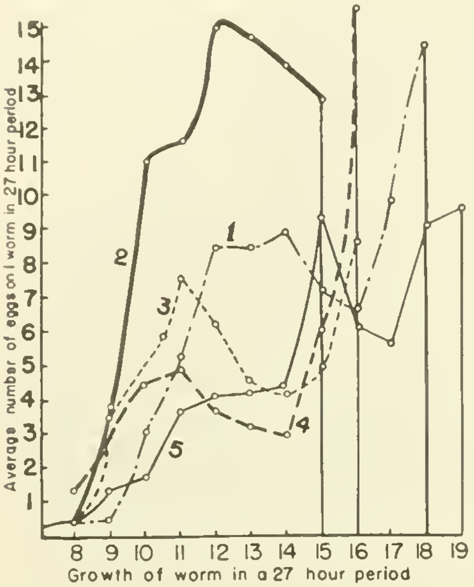

Fig. 119. *Dactylogyrus vastator* Nybelin, dependence of the tempo of the deposition of eggs on the age of the worms. Observation on egg deposition of worms located in natural conditions on the gills of very young carp. Fish Industry "Ropscha," Leningrad region (According to Izumova, 1953). 1--Very young fish. 2--Young fish no. 2. 3--Young fish no. 3. 4--Young fish no. 4. 5--Young fish no. 5.

p. 109 An important factor to the understanding of the nature of the life cycle of *D. vastator* is that in natural conditions the levels of infection in the host fluctuates, not only with the season of the year, but also with the age of the Carp. Thus, according to the data of Lyman (1951b) infection of the fishes takes place first at the age of not less than 10 days and mainly toward the end of the first month of their existence. These data are substantiated in the experimental studies of Izumova.

During the following two months of the life cycle of the Carp, the percentage of infection and the number of the individuals of the parasite increase very greatly and later toward the fall-winter period, it (*D. vastator, nobis*) is encountered also among the older ages of the fishes on a considerably smaller number of individuals and in a decreased percentage of infection. The reasons for these seasonal age changes in the nature of infection have not been clarified and can be interpreted differently. Thus, one can suppose that a relative age immunity enters into play here, which, however, seems improbable to us. In our opinion, the reasons for this phenomenon lie in the range of conditions for existence among various adult categories of the host, and in the lesser possibilities of the contact of the latter with free-swimming larvae, *D. vastator* (see also further page 110). It is possible, however, that different factors take place and also that the tissues of the gills of the carp of different ages possess unequal tenderness, and by this very fact the possibilities of attachment of the larva to the gills in different ages of the carp are not the same.

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[1] Contrary to her data, all information about the deposition of eggs of *D. vastator* cited in the works of Groben, Lyman and others has no significance to the understanding of the life cycles because it concerns the deposition of the eggs by worms which are located in artificial and obviously completely unfavorable conditions. These data basically can be utilized only for the clarification of the rate of the production of the eggs.

Thus, the life cycle of *D. vastator* consists of three stages closely connected with the cycle of the host and with the yearly changes of the conditions of the body of water. Reproduction of *D. vastator* starts in the early spring and continues for the entire summer during which a significant number of generations are passed, and during the period of the warmest months the number of parasites increases extremely. As a result of the fact that toward the period of mass emergence of the free-swimming larvae the developing fish of the year are susceptible to infections and are located in places where a significant deposition of the eggs of *D. vastator* occurred, the bulk of the latter at first develops on young-of-the-year fishes and not on the older ones which go away into places which are not suitable for infection. Toward the fall the tempo of reproduction and the speed of embryologic development decrease and finally the period of winter depression begins during which the small number of worms which were preserved on the fishes decreases to such an extent that toward the spring only isolated individuals remain. In the spring the period of reproduction of the surviving individuals (including those which spend the winter without reaching maturity in the fall) begins, and the infection of fishes takes place first by the larvae which emerge from the hibernated eggs, and then from the eggs deposited by the surviving adults. In the beginning, the infection develops among the older ages of fishes and only later in the newly appearing generation. Thus, in natural conditions the crowding of fish is less and the conditions for contact between the larvae of *D. vastator* with different ages of the host are not the same and basically insufficient so that the infection of the fishes is usually small and the outbreaks of fatal epidemics are practically absent. The result is different in culture farms where artificial conditions inevitably lead to the increase of infection of earlier ages which causes epizootics of *Dactylogyrus*. Hence, the necessity for constant active reference of parasitologists to the conscious (detectable, *nobis*) change in the character of the quantity and infection of *D. vastator* in order to prevent the outbreak of epidemics.

The cycles of the majority of freshwater *Dactylogyrus* have a similar nature and differ mainly in details. Thus, *D. solidus* Akmerow is apparently a more cold-loving type (Bauer and Nikolskaya, 1954), and, in this connection in the conditions of our carp farms the nature of the change of the infection of fishes by it is somewhat different and the maximum quantities of the parasite fall at a time of the summer period. p. 110

Among Dactylogyrus the life cycle of D. iwanowi Bychowsky, which parasitizes the Far-Eastern Rudd--Leuciscus brandti (Dyb.), stands apart.

Ugay, or Rudd as it is more often called in the Far East, is the only marine representative of carp in our fauna. It is a typical anadromous species. During its entire life it is encountered in the sea, sometimes far away from the mouths of the rivers and entering into the latter only for spawning: "In the Suyfun and other rivers entering into Peter the Great Bay it ascends (the rivers, nobis) when the ice begins to melt and sheds roe in the beginning of May-June and during the summer up to September, and the individuals which finish spawning during the summer then descend into the sea; the immature ones are encountered all year round at the mouths of the estuaries; the young ones, having hibernated in the river and having reached 7 to 9 centimeters in length, descend into the sea" (Berg, 1949).

Although very insignificant and based predominantly on fixed material, our data show that infection by D. iwanowi takes place in the river period of the life of the Rudd and that mainly the young individuals which are descending into the sea are infected. The worms live on their hosts more than a year, reach maturity during the marine period of their lives, and during the approach of the host to the river begin an increased deposition of eggs. What remains to be explained is whether a deposition of eggs takes place during the marine period of life of D. iwanowi and what is the fate of these eggs. Apparently, even if this deposition takes place, the larvae emerging from the eggs practically do not infect Rudd, because conditions exclude the possibility of the encounter of the larva with its host. Likewise, the secondary infection of the adult individuals which takes place in the fresh water is a more rare occurrence than the infection of the young, for the same reasons as were indicated for D. vastator. Thus, the life cycle of D. iwanowi (Fig. 120) (Fig. 120) already has a much more complex character and is adapted to the peculiarities of the biology of the host.

We observed a singular life cycle in the parasite of the Zheltoperaya flounder (Green-finned Flounder, nobis), Limanda aspera (Pallas)--Protancyrocephalus strelkowi Bychowsky (Fig. 131). This species is encountered almost exclusively on mature flounders at ages ranging from less than a year to three years mainly along the coast or the zone close to the coast of the sea and at depths of up to 2 meters. For the understanding of the life cycles of Pr. strelkowi it is necessary to explain briefly the data concerning the biology of its host, the Zheltoperaya flounder.

The Zheltoperaya flounder is widely distributed in the Far East and is encountered at different times of the year at different depths starting from the littoreal zone to 180-200 meters and even deeper. The mature individuals, i.e., the age categories from four years and above, maintain themselves in the winter at great depths and migrate into shallow waters with the arrival of spring where at depths of from 8 to 20 meters they begin to spawn. Spawning usually takes place in June-July, after which the adult individuals spend a certain time in the same region feeding vigorously and then towards October-November begin migrating toward the depths. The younger age groups also perform analogous migrations, but begin them earlier and proceed toward the shore at shallower depths and in the fall depart not so far as mature individuals. Thus, the majority of young p. 111 flounders hibernate in depths of 15 to 20 meters. The roe of the Zheltoperaya flounder is pelagic and the larvae which emerge from it direct themselves toward the shore, and undergo a metamorphosis in the zone very close to the shore and remain until late fall. The migrations of flounders are closely linked with the temperature regime of the sea (Moiseev, 1946).

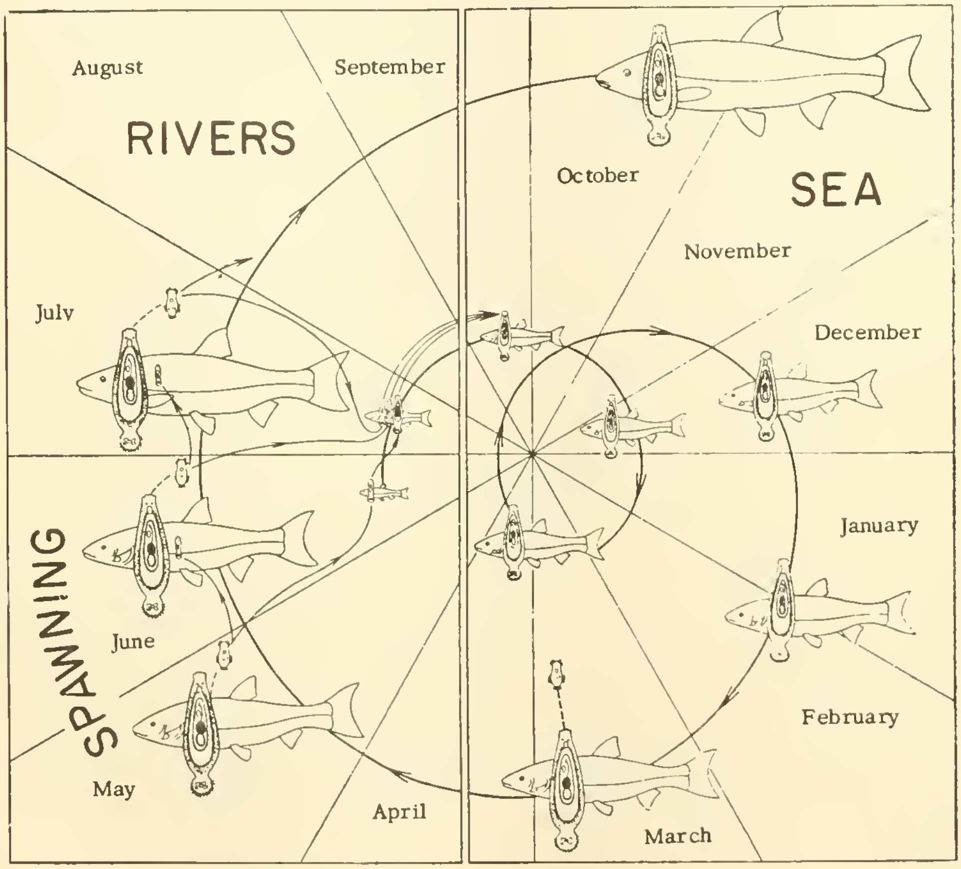

Fig. 120. Dactylogyrus iwanowi Bychowsky, schematic representation of the life cycle, somewhat simplified (the period of hibernation of the young Leuciscus brandti in the river is not indicated; and for the sake of convenience it is understood that the young ones descend into the sea completely). Explanation in text.

According to our observations the infection of the flounder takes place only in the littoral zone and the reproduction of Pr. strelkowi takes place not during the entire warm period but mainly at the end of July and in August. This reproduction has a mass character. From our diaries it is apparent that in the Bay of Anama at the Island of Shikotan the accretion of the quantity of larvae of Pr. strelkowi on flounders of 13-17.5 centimeters in length (that is, approximately, 2- or 3-year olds) takes place at a fast tempo. The development of eggs lasts from 8 to 11 days and the further development of the larvae on the flounder continues very quickly, apparently with the same speed as among the *Dactylogyrus*. Taking into consideration that we found several hundred larvae that were in similar stages of development on the gills of the flounder at the same time and also taking into consider- p. 112 ation the small number of adult worms, one can consider that the deposition of eggs takes place in large quantities during a relatively short period. The infection of large individuals also takes place but both the percentage of infection and the quantity of parasites among them are very low. Thus, in the Bay of Anama we found *Pr. strelkowi* in flounders of 28 to 32 centimeters in length (4 years and older) only 3 times among the large numbers of fishes examined and, in all cases, bearing a single individual each. From what has been said we can establish that the life cycle of this worm is adapted to the conditions of the littoral zone where *Pr. strelkowi* is constantly present on its host. Infection of mature individuals is almost lacking precisely because of the fact that adult flounders either completely or almost completely avoid these depths. We could not explain the continuity of the life of the worms with precision but it is evidently not less than 8 months, because the three-year-old flounders depart into depths when they are highly infected and toward spring they return either completely uninfected or infected only rarely. Thus the infection takes place only among the young groups of fishes which do not migrate very far and which return to the shore earlier. Consequently, in the example of *Pr. strelkowi* we see a special type of the adaptation of the life cycle to a determined age composition of the host and to a determined place of habitation within the limits of the range of the latter. In the case of *D. vastator* Nybelin, we could not precisely indicate the reasons for the weak infections of the older ages (of the host, *nobis*) and express only the hypothesis that here the absence of contact between the free-swimming larvae and the host and not an age immunity is of primary significance. But, in the case of *Pr. strelkowi*, we can ascertain that the absence of infections in older ages (of the host, *nobis*) is a result not of immunity, but of special correlations of the life cycles of the parasite and the host.

The life cycle of *Diplozoon paradoxum* Nordmann, a widely distributed and well-known parasite of freshwater carp fishes appears to be rather complicated. The basic stages in the life cycle of *Diplozoon* were described by early researchers, mainly by Zeller (Zeller, 1872c). Certain observations which coincide in principle with Zeller's were also conducted by us. In the winter period the adult *D. paradoxum* are located on the fish in an inactive state. According to Zeller, their sex system not only does not function but also their sex products are as yet developed very weakly. Thus, Zeller observed that a quick development of egg cells and vitelline cells takes place in the spring with the natural rise of the temperature of the water, or during the artificial transfer of the parasite with its host into a warm aquarium even in the winter, and that egg forma-

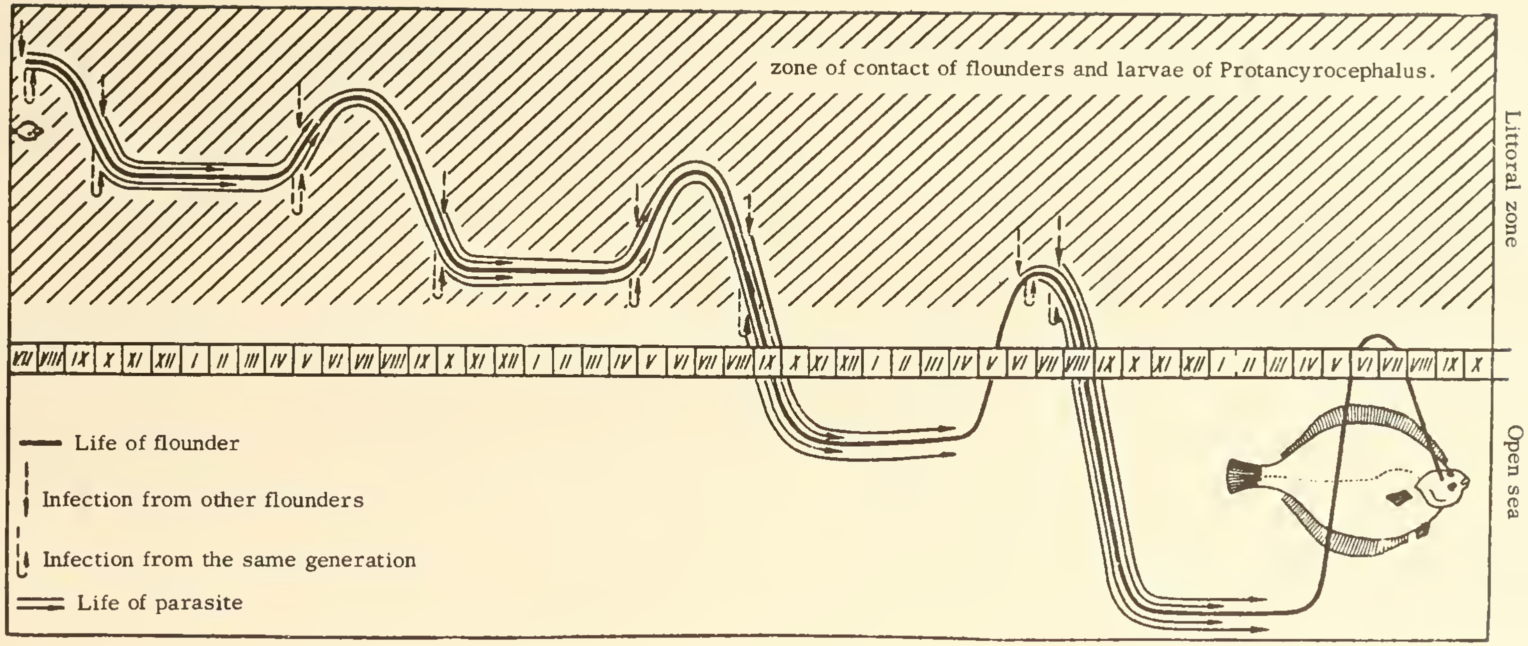
zone of contact of flounders and larvae of Protancyrocephalus.
Littoral zone
Open sea
VII VIII IX X XI XII I II III IV V VI VII VIII IX X XI XII I II III IV V VI VII VIII IX X XI XII I II III IV V VI VII VIII IX X XI XII I II III IV V VI VII VIII IX X
Life of flounder
Infection from other flounders
Infection from the same generation
Life of parasite

Fig. 121. Protancyrocephalus strelkowi Bychowsky, schematic representation of the life cycle. Explanation in text. The Roman numerals equal months of the year.

tion has begun on the fifth or sixth day. Our observations on the sex system of D. paradoxum give a picture similar to the one described for Polystoma integerrimum Froelich (see page 82). The worms examined during the winter have a fully developed sex system, and in the spring period it begins to act very quickly without any special period of accelerated development of sex cells. The change to the active state takes place much slower than in P. integerrimum, which is understandable when one takes into consideration the gradualness in the increase of temperatures in bodies of water where parasites and their hosts are located. The reproduction of D. paradoxum which begins in the spring continues almost the entire summer but the intensity of the deposition of eggs in May-June is significantly higher than in the following months. The eggs of D. paradoxum basically remain on the gills of the host, and Zeller observed up to 100 in each fish with 3 mature parasites under artificial conditions. The larvae emerge from the deposited eggs on the 12th to the 17th day according to p. 114
Zeller (according to our data, 9-10th day) and after a short time they infect fish. The diporpa larvae which settle on the gills live for a certain length of time singly and their growth develops rather slowly. After reaching a determined stage of the development of the attaching apparatus (2-3 pairs of clamps), a large part of the larvae ceases further growth if it doesn't meet the same larvae with which it unites in pairs, grows together and continues mutual development. The larvae which remain single live for a sufficiently long time, but all perish toward the winter. The individuals which united in pairs begin to grow much more quickly than the single ones and toward the spring of the following year they reach maturity. As is apparent from what has been said before, the critical moment in the life of D. paradoxum is the union of a pair of individuals, without which further development is impossible. Taking into consideration that the periods of the emergence of the larvae from the eggs are greatly extended one would expect a large percentage of loss of some of the worms; however, this is not observed in nature. The reasons for this appear to be a repeatedly noticed union of the larvae of more or less different ages. Thus, relatively slow growth of the larvae is an adaptive peculiarity to the singular life cycle of D. paradoxum. All in all, the life cycle of the latter (Fig. 122) has a number of primitive traits characteristic of the forms with extended egg deposition, and just as many highly specialized traits which are determined by the peculiarities of the sex cycle. In addition to what has been said before, one must note still another peculiarity in the nature of infection of the host: Younger hosts are infected less than older. Thus, those of less than a year are completely free of D. paradoxum, the yearlings either are completely uninfected or infected exceptionally rarely and weakly and are often infected not by pairs but by a single diporpa. How this phenomenon can be explained one cannot say exactly; however, we are certain that here take place the same circumstances about which we have often spoken earlier, that is, different places of location of older and younger fish. In connection with this is the fact that the eggs of D. paradoxum are found on the gills the fishes of younger ages, which as a rule keep themselves separate from the older ones,

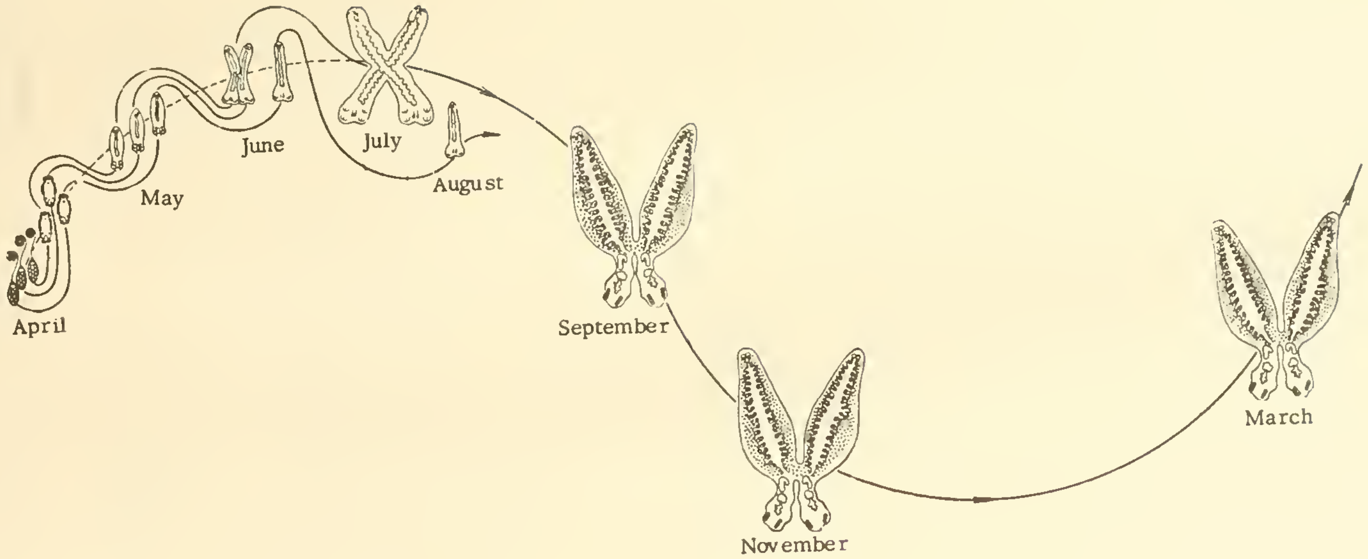
April
May
June
July
August
September
November
March

Fig. 122. *Diplozoon paradoxum* Nordmann, schematic representation of the life cycle. In addition to the normal development, the fate of the little larvae which did not pair up is indicated in the diagram. Explanation in text.

p. 115

have very little probability of being infected with the larvae of D. paradoxum.

Certain observations of the life cycle of Mazocraes alosae Hermann were conducted by us on the Caspian Sea during 1931-32. The hosts of this parasite in the Caspian Sea are numerous types of herring, among which we dealt basically with Alosa brashnikovi (Borodin), A. saposhnikovi (Grimm), and A. caspia (Eichwald) in the region of the Island of Sara. The study of the worms during May and June disclosed a strong cyclical nature in the period of reproduction of this species and consequently a quite complex character of the life cycle. According to our observations the herring bears only large mature M. alosae on their gills until the middle of May, and the latter do not form or deposit eggs. In our diaries there are notes that even in artificial conditions we were unable to obtain deposition of eggs from the worms. The beginning of the formation and deposition of eggs was first noticed in the beginning of the second half of May, and this process took place in a very turbulent fashion. The eggs are deposited by worms on the gills and attach to them very tightly by the tens and even hundreds on a single fish. From experimental data, we know that the deposition of eggs of M. alosae takes place during 4 to 6 days. Taking into consideration that in nature temperature conditions are different, we can consider the periods of development of eggs in nature equal to 8 to 10 days. This fully corresponds with our observations. Thus, the first depositing individuals of M. alosae were noticed p. 116 May 19th and already 8 days later we discovered larvae on the Kislerov Herring which had just settled.[1] The number of the larvae which settled on the gills of the fishes is not very great. According to our notes, it fluctuates from five to fifty--mostly around 20, i.e., it corresponds to the number of adult worms normally observed in nature in other periods of the year. The period of infection of herrings apparently is not very long--within limits of a month or less. The further growth of the settled larvae takes place fairly rapidly; thus already a fortnight later (13 June) we found young M. alosae with three pairs of clamps and with the fourth in the process of inception. Thus, the complete formation of the attaching apparatus takes place during 15 to 20 days, on the average.

In view of what has been said before and also from the observations on the nature of infection of herrings of the genus Alosa from the Caspian and Black Seas, one can visualize the life cycle of M. alosae more or less exactly (Fig. 123). As is known, our southern herrings approach the shores or enter the rivers for spawning for relatively short periods, mainly in April-June. After that they descend from the rivers into the sea, or depart from the shores and maintain themselves in the depths: according to the data of Svetovidov (1952), in a scattered fashion and, in addition to that, the younger ages keep themselves separate from the old ones. Thus, the basic favorable time for cross-infection of the host is the period of the approach of the herring toward the shores for spawning. The mass deposition of eggs of *M. alosae* coincides precisely with this period. Undoubtedly the probability of infection of the host would have been exceedingly small if the eggs were deposited directly into the water, for during the migration of the herring their scattering would have been exceedingly great. Thus, it is clear what a great adaptative significance the deposition of these eggs on the gills of the host by *M. alosae* has. From this, certain peculiarities of the infection of the host of different ages emerge. *M. alosae* is encountered only on adult fishes starting with three-year-olds (let us remember that as a rule the majority of Caspian herring spawn at this age for the first time and that two-year-olds spawn only in rare cases), that is younger ones are not infected with *M. alosae,* which is easy to understand because the contact between the younger and older ages of the herring is very insignificant, if it isn't practically absent all together. It isn't clear whether the less than one-year-old or the yearling herring are in a position to be infected. In nature they never meet with larval *M. alosae* capable of infecting them, whereas the two-year-olds have more chances to enter into contact with the older ages there and consequently have a greater possibility of being infected. Actually in rare cases we observe this in nature. The question about infection of fishes in fresh water appears unclear in the life cycle of *M. alosae*. We have no factual observations on this but it seems to us that, taking the biology of the host into account, this possibility is not excluded. Further research will verify the correctness of the supposition.

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[1] In 1955 on the Isle of Sara we observed egg depositing individuals of M. alosae even earlier--May 13.

Apparently the life cycles of two species of *Octostoma* which parasitize the Japanese mackerel--*Pneumatophorus japonicus* (Houttuyn) are close to the life cycle of *M. alosae*. In nature we see that *Oct. scombri* (Kuhn) and *Oct. minor* (Goto) (Fig. 124) are encountered only on adult fishes. beginning with two-year-olds. At the same time, the parasites which are encountered are always of one size--fully matured. Hence, p. 117 one can suppose that the multiplication and deposition of eggs of both species have a periodic nature.

The Japanese mackerel usually maintains a depth of 20 to 40 meters in the open sea and comes to the shores in large schools for spawning in May and June. The spawning extends approximately from the middle of June to the middle of July within 5 to 6 miles of the shore. The young ones which emerge from the roe wander toward the shore where they remain the entire summer, going to the depths in the late fall and returning (to the shore, *nobis*) early (the next spring, *nobis*). In such a fashion, contact between the early ages and the mature mackerel is absent. Because of that and also of the fact that, as among *M. alosae,* the eggs of both types of *Octostoma* are detained on the gills of the host, one can expect that the

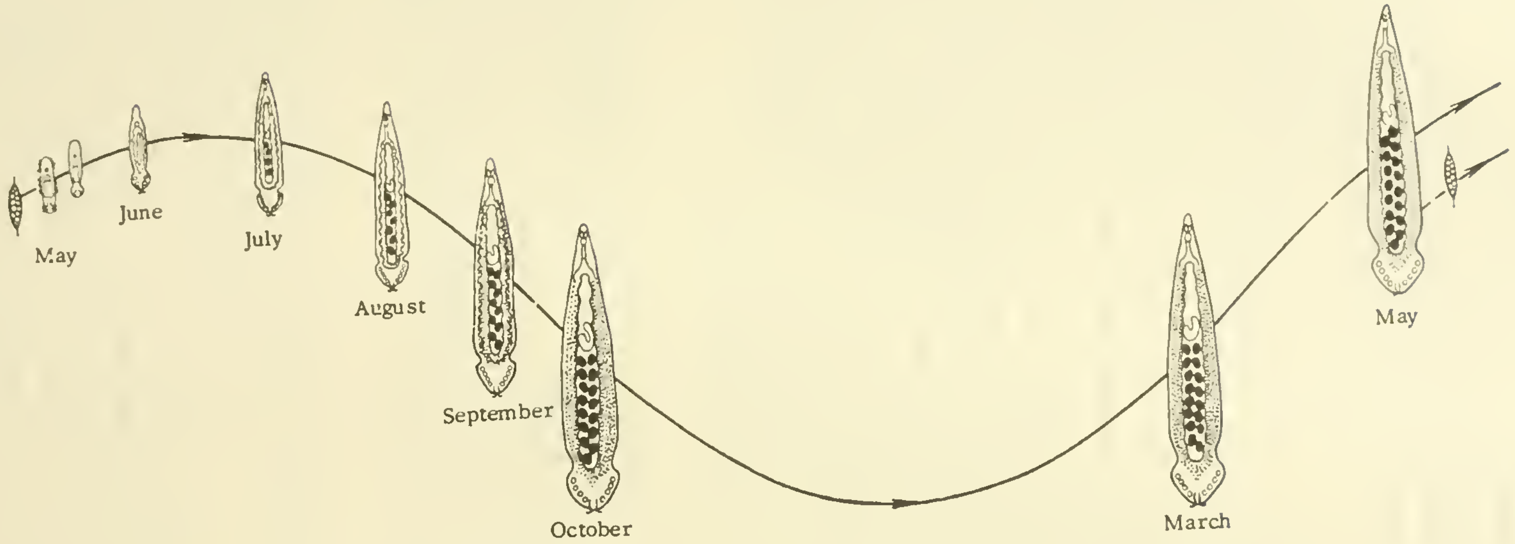
May
June
July
August
September
October
March
May

Fig. 123. *Mazocraes alosae* Hermann, schematic representation of the life cycle. Explanation in text.

peculiarities of the infection of the mackerel correspond to those of the herring parasite, and the life cycles of all three species are actually very close. We cannot fail to notice, also, the systematic proximity of both genera of monogenetic trematodes.

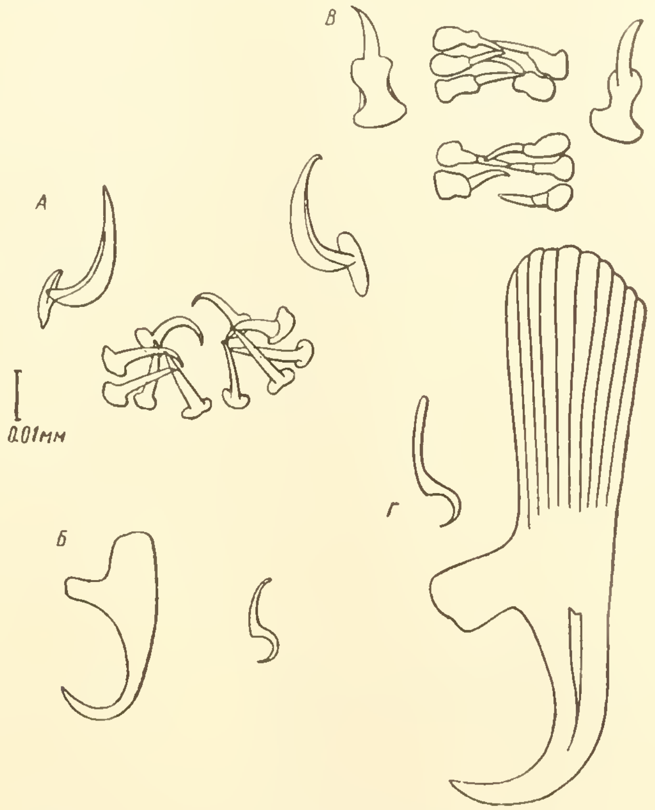

Fig. 124. *Octostoma* sp. sp. from the gills of *Pneumatophorus japonicus* (Houtt.) from the region Yablochnoii (southern Sakhalin, Sea of Japan). A--Armature of the copulatory organ of *O. minor* (Goto); B--Middle hooks of the attaching disc of *O. minor* (Goto); C--Armature of the copulatory organ of *O. scombri* Kuhn; D--Middle hooks of the attaching disc of *O. scombri* Kuhn.

Interesting observations on the life cycles of *Microcotyle gotoi* Yamaguti were successfully conducted during works on Southern Sakhalin in 1946 and continued in 1949 on the Island of Shikotan. *M. gotoi* parasitized natural marine fishes of the genus *Hexagrammos*, mainly on *H. octogrammus* (Pallas) in Southern Sakhalin and on *H. lagocephalus* (Pallas) near the Island p. 118 of Shikotan. In our opinion, the data on the biology of these fishes are still insufficient, and because of that we should first show the materials which we have on the life cycle of *M. gotoi* and attempt to compare them with information available about the Terpug (rock, trout, starling, *nobis*).

In summertime up to the middle of August only mature parasites are encountered on both types of fishes and (then, nobis) only on older fishes. Thus, M. gotoi is encountered on H. octogrammus starting from two-year-olds (the lengths of the fishes are from 18 centimeters) and on H. lagocephalus--among fishes with sizes from 20 centimeters (apparently also two-year-olds). Mainly toward the middle of August we observe Microcotyle on both fishes with a large number of eggs in the uterus which are deposited simultaneously by the worms and then a new portion of eggs begins to accumulate in the uterus which was just emptied. An especially intensive formation and deposition of eggs of M. gotoi takes place during this period. This process continues until the second half of September when apparently it ceases or in any case slows down considerably. Emergence p. 119 of larvae and the infection of fishes from the eggs deposited in the water begins at the beginning of the third ten days in August in Southern Sakhalin and in the first ten days of September in Shikotan. Inasmuch as the larva which has just emerged from the egg does not yet have clamps and since the latter are incepted gradually in proportion to the growth of the larva we can, on the basis of the structure of the attaching armature of the larvae, judge about the periods of infection of the host, the intensity of infection and also about the length of time during which it takes place. In the beginning, the intensity of new infections builds quickly and then gradually decreases until young stages are almost completely absent. According to the time, it is apparent that in outhern Sakhalin this process is most intensive at the end of August--the beginning of September, and on Shikotan--somewhat later. A strong decrease in infection takes place apparently in both regions in October (on Shikotan we did not observe the end of this process). Thus the emergence of larvae from the egg takes place very intensively only from 15 to 20 days, although it extends generally up to a period of almost one and one-half months.

The infection of fishes takes place unequally according to ages. The most strongly infected are yearlings, which until that time were completely free of Microcotyle. Along with them the older stages are also infected, although in much smaller numbers and percentages and by a smaller number of parasites. In this case, a great role is played by the location of the fishes of different ages. Thus, fishes up to 20 centimeters in length, i.e., until the age of two, keep much closer to the shore all the time, whereas the older ones are encountered in shallow places in much smaller numbers and apparently rarely after spawning. After the infection of the fish, the worms grow rather slowly so that at the most after ten days they have 10 to 15 clamps instead of the 38 to 42 pairs characteristic of adults. Apparently the full development of the attaching apparatus is delayed until the late fall and the worms reach maturity towards the spring-fall of the following year. The data obtained fully correspond to the sketchy information about the biology of the Terpug (Rock, Trout, or Starling, nobis). It is known that the latter does not reach maturity before the age of two years. The adults usually maintain themselves at depths of more than 10

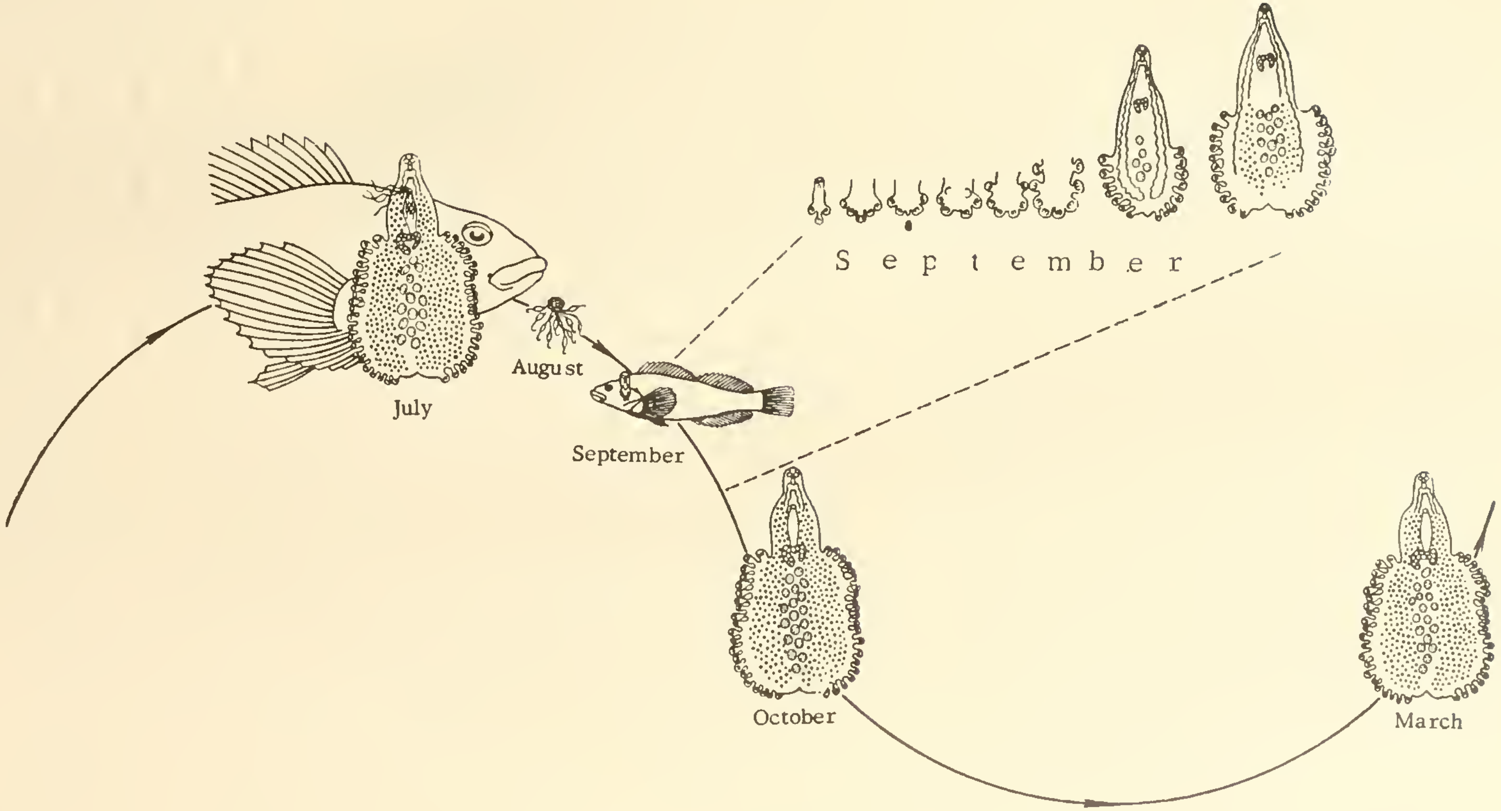
September
July
August
September
October
March

Fig. 125. *Microcotyle gotoi* Yamaguti, schematic representation of the life cycle. Explanation in text.

to 15 meters and approach the shore only in spring. Spawning apparently takes place in August[1] and during that time the adult individuals approach the shore very closely. After spawning, adults return to the greater depths. The young fishes in ages up to two years basically maintain themselves in shallow water the entire summer, almost right by the shore, and in late fall migrate to greater depths. Juxtaposing the data on biology of fishes with the parasitological data, we see that the life cycle of *M. gotoi* (Fig. 125) is fully adapted to the peculiarities of the life cycle of the fishes. Also the reasons for the absence of larval stages and developing worms on the adult fishes until fall and also the absence of infection of young ages become clear. At the same time, the data cited indicate that the life span of *M. gotoi* individuals is not less than a year and most likely is even longer, because on adult two-year-olds we find worms of somewhat lesser size than on the older fishes.

The life cycle of *Polystoma integerrimum* Froelich is extremely complex. Excellent observations of *P. integerrimum* Froelich, which parasitizes different frogs, mainly *Rana temporaria* L., were expressed in the works of Zeller (Zeller, 1872a, 1876) and Gallien (Gallien, 1935). We also have considerable material. It was obtained as result of three-year observations p. 121 in 1927 to 1929 in the region of the Peterhof Institute of Natural History. Because of the differences of geographical points of research between our material and the information of the above-mentioned authors, there are a number of differences; mainly in the lengths of different processes. Because of this, we shall outline the life cycle of *P. integerrimum* in general traits and then reproduce certain calendar (chronological, *nobis*) data based on our and Gallien's observations. The examination of the life cycle (Fig. 126) begins best with the winter period of the year and with fully adult individuals--4 to 5 years. At this time all the worms have a fully developed sex system completely ready to begin functioning but still inactive. The worms are located in the urinary bladders of the hibernating frogs. In early spring as the latter emerge from that portion of the body of water in which hibernation took place, the sex system of *P. integerrimum* begins to function and a few days later, during which the "excision" of egg cells (see page 84) takes place, egg deposition begins. Toward that time the frogs pair and again depart into the water to a place where a day or two later they deposit roe. The eggs of *P. integerrimum* are deposited in the same place and almost at the same time as the roe of the frogs. However, the deposition of the roe terminates somewhat earlier than the deposition of the eggs of *P. integerrimum* because the former usually takes place within 6 to 15 days

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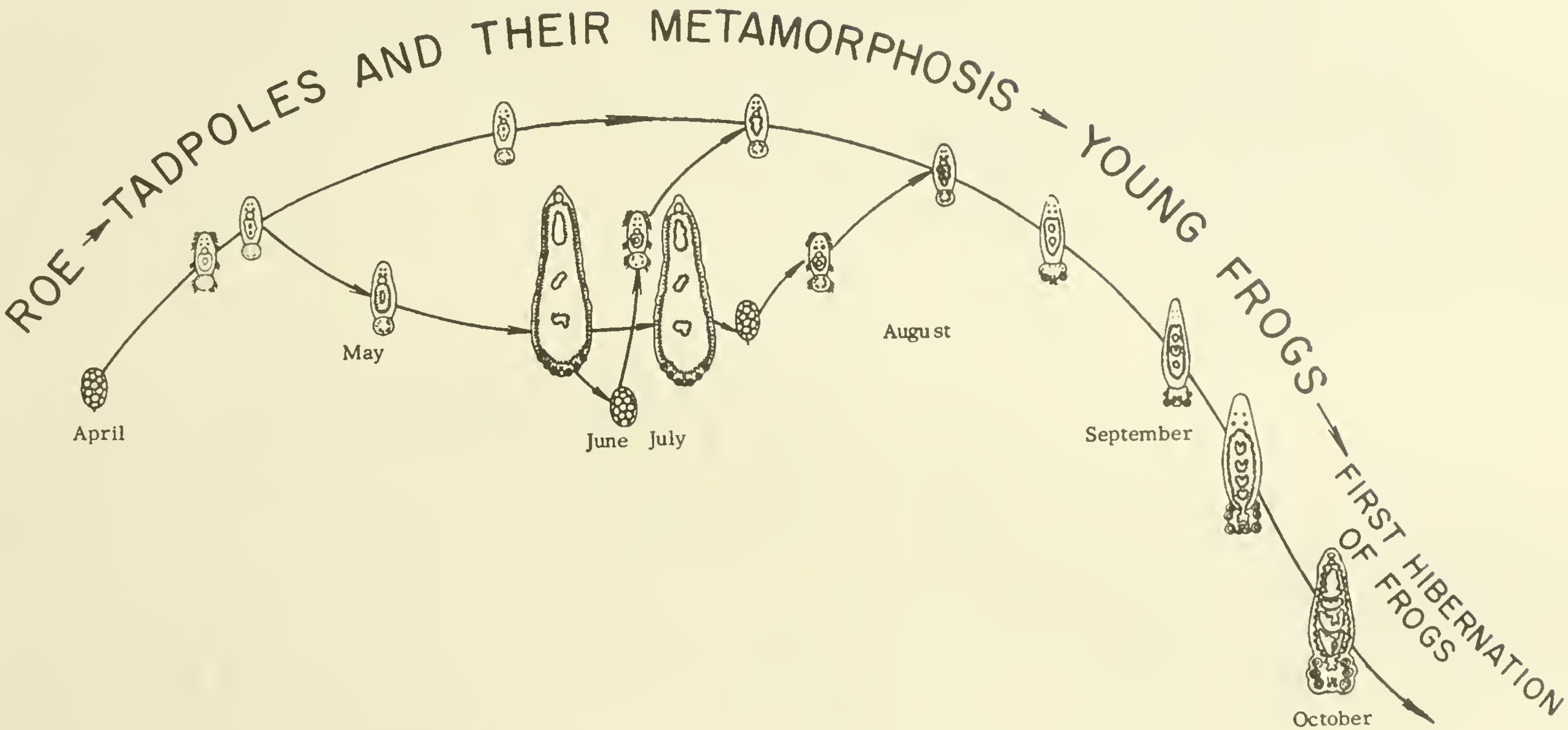
[1] It is known precisely that near Hokkaido *H. octogrammus* spawns in the second half of August; near Shikotan the individuals of *H. lagocephalus* which had just spawned were encountered from the end of August.

and the latter from 10 to 20 days, and sometimes it is delayed for a certain additional period. The development of eggs of *P. integerrimum* in natural conditions is rather lengthy. Depending upon temperature conditions, it lasts from 20 to 30 days in the Leningrad region and from 40 to 50 days in France (according to Gallien). The free-swimming larvae emerging from the eggs seek their hosts, which happen to be tadpoles which at that time are undergoing different stages of development, starting with the appearance of inner gills. The fate of the larvae becomes different after their attachment on the gills of the tadpoles. If the larva attaches itself to the gills of a very young tadpole it begins to feed intensively and grow fast, changing into a special mature form, the so-called "gill" *P. integerrimum.* In the case when the larva falls on more mature tadpoles they feed less intensively and grow more slowly without the development of the sex system (their fate will be described somewhat later). The "gill" *P. integerrimum* reach full maturity 20 to 25 days after the settling of the larvae on the gills of the tadpole and from that time begin to produce eggs. The gill form is very interesting in structure because it differs significantly from *P. integerrimum* from the urinary bladder. The gill *P. integerrimum* (Fig. 127) has a less distinct, so to speak, broadened configuration of the body and the attaching disc is not delineated from the body, the interior organization is also sharply distinct. The intestinal tract has a small number of lateral growths and interior anastomoses and the location of both is less regular than among *P. integerrimum* from the urinary bladder. There are especially significant differences in the structure of the sex system. The ovary of the gill form is very long and almost straight with a flask-like widening at the anterior end filled with rapidly developing oögonial cells. Oöcytes in the ovary lie one after another in its longer part and are efferred (expelled, *nobis*) from the ovary according to their degree of maturity. Generally the shape of the ovary of the "gill" *P. integerrimum* resembles that of the young, still immature *P. integerrimum* of the urinary bladder (Fig. 128). Among the gill forms the vaginal ducts are completely absent and actually, so to speak, there is no uterus as among many of the lowest monogenetic trematodes, but only an oötype in which a single egg is formed at a time p. 124
which is immediately carried outside. According to the data of Gallien, the *ductus genito-intestinalis* is absent among the gill type of the parasite, and apparently it is really so. The male sex system is represented by a round testis and a seminal duct which opens into the copulatory organ of identical structure to the one of *P. integerrimum* from the urinary bladder. According to Gallien, the seminal duct is absent and the copulatory organ is not connected in any way with the testis, so that it represents, in such a fashion, only a rudimentary remnant. According to Gallien, fertilization takes place through a special duct uniting the male and female sex systems. In his time Zeller also wrote about this duct. Our observations do not substantiate these data. Fertilization of gill forms takes place just as among lowest monogenetic trematodes--not through a special canal, but through the oötype. The life span of the gill form coincides with the period of existence of the inner gills of the tadpole--with their disappearance, the "gill" *P. integerrimum* perishes. The deposition of eggs


ROE → TADPOLES AND THEIR METAMORPHOSIS → YOUNG FROGS → FIRST HIBERNATION OF FROGS
April
May
June
July
August
September
October

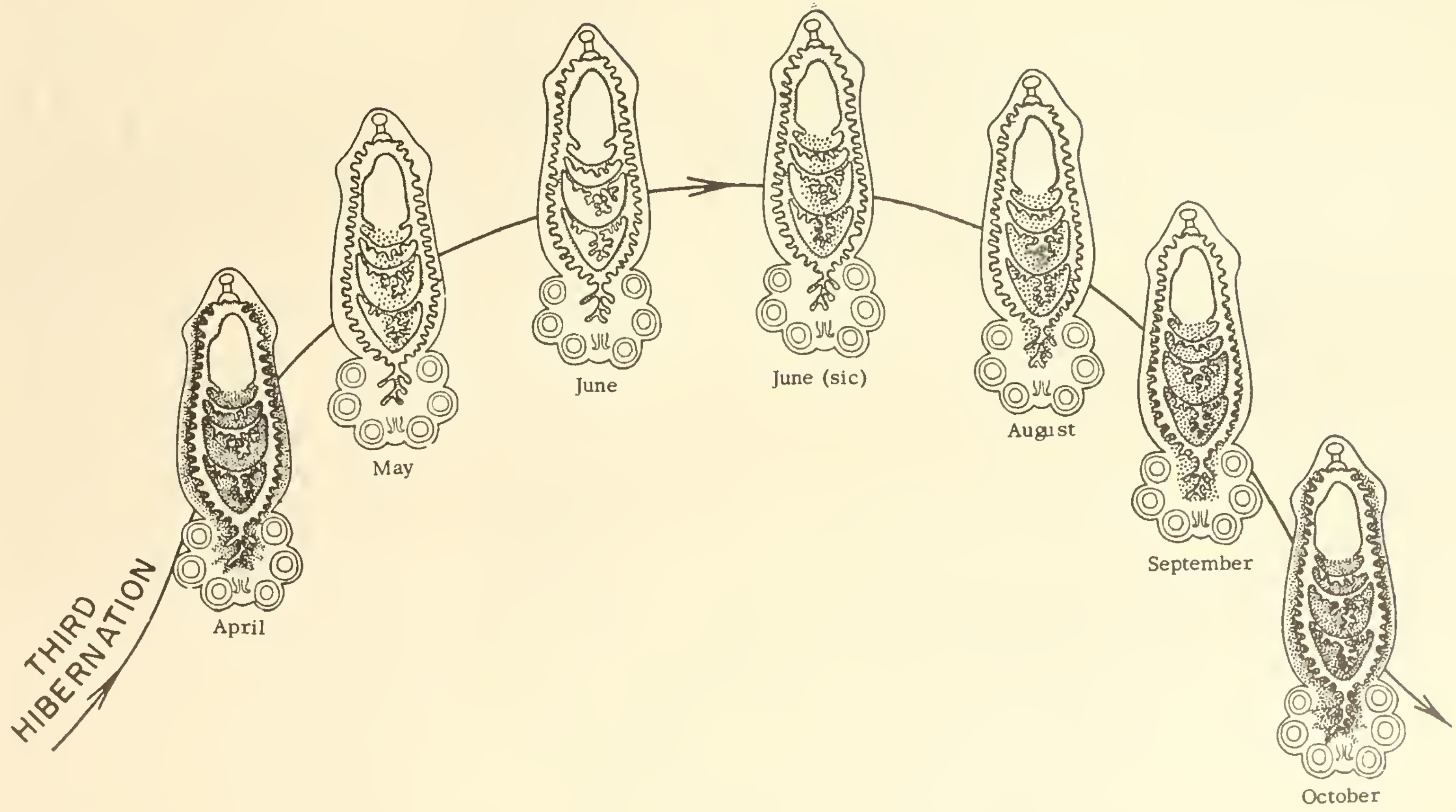

THIRD
HIBERNATION
April
May
June
June (sic)
August
September
October

Fig. 126. *Polystoma integerrimum* Froelich, schematic representation of the life cycle. On the top--first year of existence; bottom--fourth year of existence.

among this form, which starts with the appearance of the approach of maturity, continues until the very death of the worms. The free-swimming larvae emerge from these eggs after approximately 15 to 20 days because at that time the temperature conditions in the body of water are more favorable. The larvae of the gill forms, just as the larvae of P. integerrimum from the urinary bladder, attach to the gills of the tadpoles. Their further p. 125 fate is the same as that of the larvae of P. integerrimum of the urinary bladder which settled on the gills of older tadpoles. Morphological differences between both are absent, and during the metamorphosis of the tadpoles they pass from the gills through the entire intestinal canal into the urinary bladder. In the urinary bladder and sometimes somewhat earlier, the larvae begin gradually to acquire the final structure of the attaching disc, which toward winter becomes fully formed with all three pairs of suckers and with a middle pair of chitinous hooks. Further growth of Polystoma takes place during the following summer and finally they reach maturity in the third year. It must be indicated that the first maturity takes place with the presence of an ovary of different form than among four-year-old worms and with testes of smaller sizes. The deposition of young mature individuals of the urinary bladder takes place just as among older ones but begins somewhat later and the number of eggs deposited is smaller.

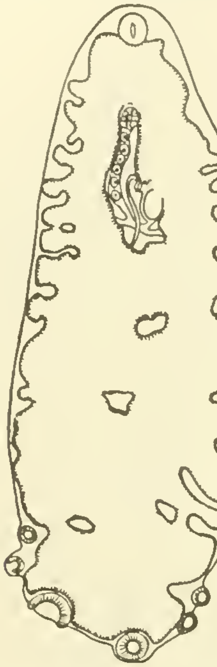


Fig. 127. Polystoma integerrimum Froelich, mature gill form from the gills of tadpoles of Rana temporaria L. from Peterhof (Leningrad region). Natural size 1.2 mm.

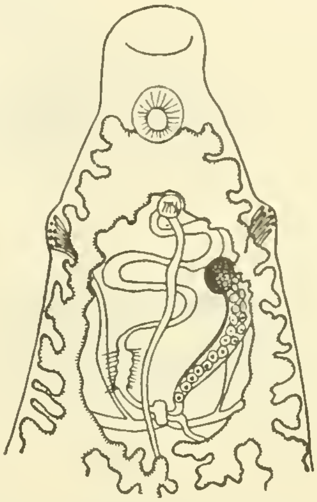


Fig. 128. Polystoma integerrimum, Froelich, young immature worm from the urinary bladder of year and one-half old Rana temporaria L. from Peterhof (Leningrad region). Natural size 1.5 mm.

In the conditions of the Leningrad region during the period from 1927 to 1929, we observed the emergence of frogs from their places of hibernation in the beginning of the third ten-day period of April and the beginning of the deposition of roe by them (see Fig. 129) as early as the 25th to the 26th of April. The latter (deposition of roe, *nobis*) continues usually for a long time, often until the end of the first ten days of May and often the first tadpoles begin to appear by this time. Correspondingly, the first copulating *P. integerrimum* were observed from the 22nd of April, and the beginning of egg deposition from the 24th to the 25th. The deposition of eggs by worms continues until the 10th to the 15th of May. The first larvae usually appear on the gills of tadpoles from the 12th to the 15th of May and adult gill forms are discovered from the first days of June at the earliest and most often from the 10th to the 15th of June. The overgrowing of the gills and metamorphosis of the tadpoles and consequently the death of the "gill" *P. integerrimum* and the migration of the larvae into the urinary bladder of the young frogs begins about the middle of July and extends for 10 to 15 days, depending upon the peculiarities of the year. The departure of the young frogs for hibernation and the cessation of growth of young *Polystoma* until spring take place before the departure of the adult frogs from hibernation (October) and in the main coincides with the cold spells of the middle to the end of September.

According to the data of Gallien, in France, (the region of the Department of Vosges near the village of Hansel) the deposition of eggs by *P. integerrimum* begins from the 25th of February and continues until the 25th of March with the maximum occurring about the 5th to the 15th of March (see Fig. 130). The emergence of the larvae and the infection of the tadpoles take place from the 15th of April to the 15th of May. The adult gill forms appear from May 10th, and their egg deposition lasts until June 15th. The eggs of "gill" *P. integerrimum* develop in 20 to 25 days, and the ones which were deposited after the first of June yield larvae which do not find tadpoles suitable for infection (metamorphosis has already begun) and for that reason are condemned to death. Correspondingly, according to the data of some authors, the roe of the frog is deposited in March mainly from the 15th to the 20th. The tadpoles emerge from the first days of April and (continue, *nobis*) approximately until its second half. The metamorphosis of the tadpoles begins from the 10th of June and basically ends before the 20th.

The difference between our data and those of Gallien consist not only in the fact that all the processes observed by him take place earlier, which is absolutely natural, but also in the fact that in our opinion some of his statements are erroneous and demand verification. Thus, first of all according to Gallien, the deposition of eggs of *P. integerrimum* in the spring significantly precedes the deposition of roe by the frogs. As is apparent from the data published by him, this difference consists of a minimum of 15 days. Taking into consideration all the peculiarities of the

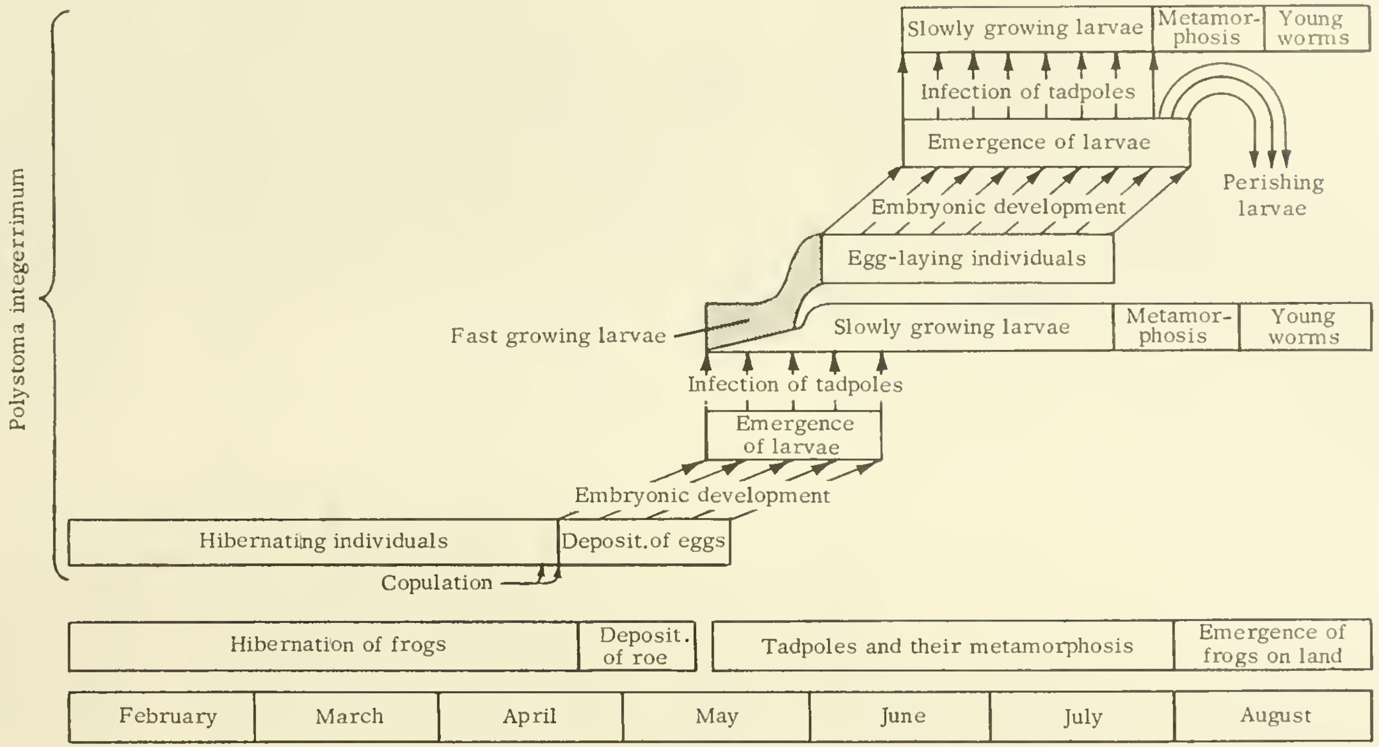

Polystoma integerrimum
Slowly growing larvae
Metamor-phosis
Young worms
Infection of tadpoles
Emergence of larvae
Perishing larvae
Embryonic development
Egg-laying individuals
Fast growing larvae
Slowly growing larvae
Metamor-phosis
Young worms
Infection of tadpoles
Emergence of larvae
Embryonic development
Hibernating individuals
Deposit.of eggs
Copulation
Hibernation of frogs
Deposit. of roe
Tadpoles and their metamorphosis
Emergence of frogs on land
February
March
April
May
June
July
August

Fig. 129. *Polystoma integerrimum* Froelich, schematic representation of the first year of the life cycle in conditions existing at Peterhof (Leningrad region).

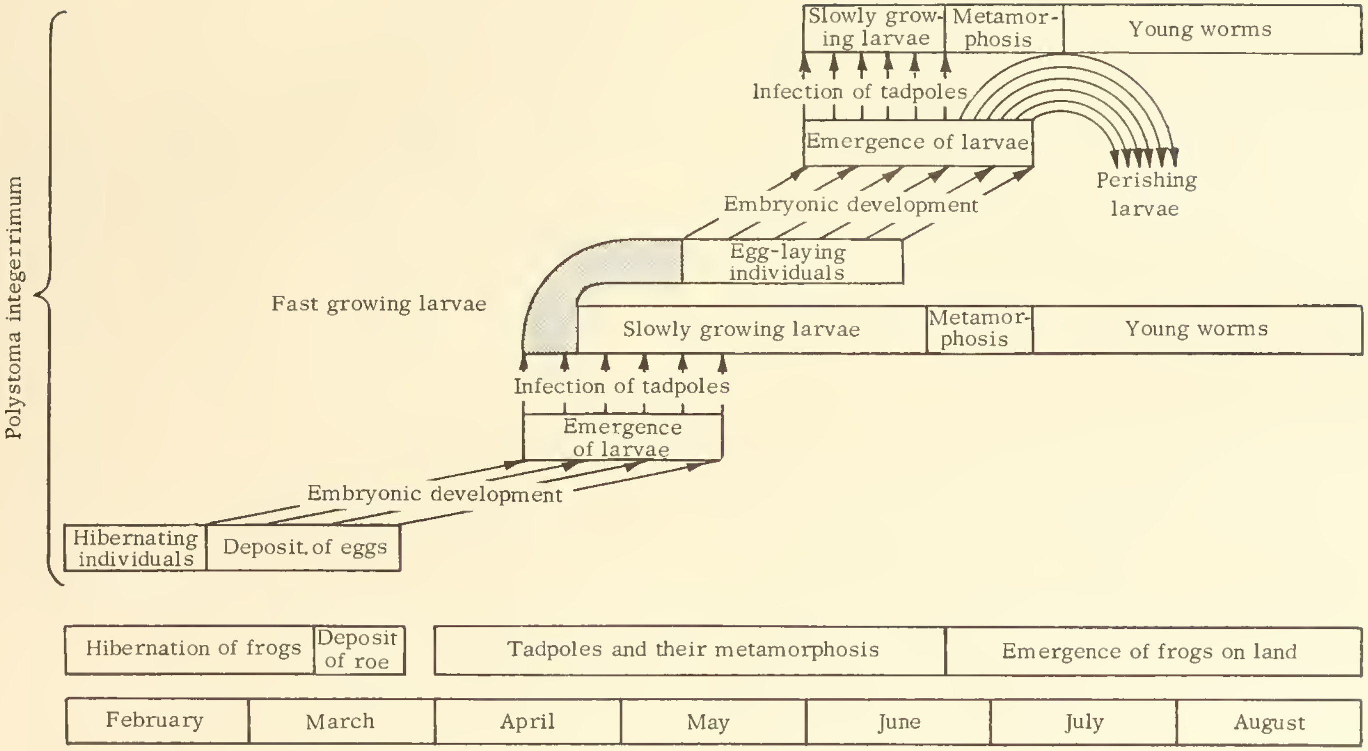

Polystoma integerrimum
Slowly growing larvae
Metamorphosis
Young worms
Infection of tadpoles
Emergence of larvae
Perishing larvae
Embryonic development
Egg-laying individuals
Fast growing larvae
Slowly growing larvae
Metamorphosis
Young worms
Infection of tadpoles
Emergence of larvae
Embryonic development
Hibernating individuals
Deposit of eggs
Hibernation of frogs
Deposit of roe
Tadpoles and their metamorphosis
Emergence of frogs on land
February
March
April
May
June
July
August

Fig. 130. *Polystoma integerrimum* Frolich, schematic representation of the first year of the life cycle in conditions existing in village of Hensel [Department of Vogesus]. (This diagram was composed according to the data of Gallien, 1935).

region of his research, this seems improbable to us because the frogs never (rarely?, *nobis*) are found at the places of deposition of the eggs fifteen days before spawning, and this possibility takes place in certain p. 128
exceptional cases but not as a rule. Hence, his data concerning the development of the eggs in nature during 40 to 50 days also seem improbable to us. The same also can be said concerning the data of Zeller. The second basic difference between our and Gallien's material is that the gill forms produce eggs which, according to our data in the main produce larvae capable of infecting tadpoles, whereas according to Gallien a large part of them develop practically as "non-breeders" because the larvae which emerge have no chance whatsoever of infecting tadpoles. Thus, in the Leningrad region the gill forms develop during the first 20 to 25 days of June, whereas in France, according to Gallien, during only 10 days in the middle of May. In connection with these peculiarities of the development of tadpoles, the gill forms lay eggs in our region in about 50 days, but in France in about 35 days. As a result, the larvae emerging from the eggs of "gill" *P. integerrimum* in the Leningrad region succeed in infecting tadpoles for 50 days and perish during the last 5 days at a maximum, whereas in France the emergence of the larvae takes place during 35 days and the infection of the tadpoles--the first 20 days and not 15, i.e., 43 per cent of the time the larvae do not find hosts for themselves and perish. It seems to us that these data of Gallien demand re-examination--we think that here are certain inaccuracies of observations. As is clearly seen from the attached diagrams (Figs. 129 and 130), all the rest agrees fairly well and shows striking lation of cycles of the host and the parasite in different geographical locations.

Before passing to certain general considerations about the life cycles of egg laying of monogenetic trematodes we do not think it would be out of place to cite an example of a break in the link between the biology of tadpoles and *P integerrimum* which we observed in 1929. In one of the ponds of the Sacred (Forbidden, *nobis*) Park of Peterhof of the Institute of Natural History, the deposition of frog roe and of *P. integerrimum* took place near the south bank. Because of the land breeze, the main mass of tadpoles which had just emerged from the roe found themselves at a distance of 2 to 3 meters from the place of spawning. As a result though 100 per cent of the tadpoles which remained (in place, *nobis*) were infected by *P. integerrimum*, 100 per cent of the tadpoles which were found to the side were uninfected. Thus, a circumstance which may at first glance appear insignificant, such as a distance of from 2 to 3 meters, did not permit the union of the links of the chain of the life cycle of the parasite.

Summarizing our information about life cycles of egg-laying forms of monogenetic trematodes, we must note first of all their increased adaptability to the cycles of the host. Even in the simplest cases, a number of peculiarities are apparent which point to the very long period of the working out of the adaptations of the parasite to the peculiarities of the life cycle of the host, and this under the completely determined conditions

of the existence of the latter. The peculiarities of the cycle of Monogenoidea find a considerable reflection in various adaptations which arise at first in the sex cycle of the animals, and also in the annual cycle of development. First of all, without any doubt, common historical orientation in the development of peculiarities of action in the sex system proceeds along the line of the gradual transition from an extended period of egg-laying to its contraction (shortening, nobis) to a greater and greater degree, which we observe among the fresh water as well as among the migratory and purely marine forms. This is especially evident among the parasites of the Amphibia, i. e., hosts which change their means of habitat from the water to the land during their life span. The reasons for this historical process, p. 129
which takes place with various degrees of intensity among various groups, are undoubtedly caused by the necessity for creation of more favorable conditions for the infection of hosts. At first sight, the presence of an extended period of egg-laying appears to be more favorable under conditions of continuous (not apportioned, nobis) egg production; however, this is completely untrue. It is wrong because the basic factor is the necessity of infection of very mobile hosts by the free-swimming larvae of the parasite. In connection with this, the presence of contact between both, in time as well as space, is indispensable. The probability of such a contact under the conditions of extended periods of egg-laying is sharply lowered, inasmuch as among a considerable number, if not the great majority of the forms, the eggs do not remain on the fish. In such a fashion the necessity, which was pointed out by us, arises for an increase in the probability of contact in time and space between the two links of parasitic cohabitation during the presence of favorable conditions of the surrounding medium for the development of eggs and the infection of the host. As we see, this is attained by the decrease of the periods of egg-laying and the concentration of the latter in a more limited region. We note also that the attachment of eggs on the body of the host serves the same purpose--the concentration at the same time of a larger number of larvae within a specific territory. The concentration of the larvae which infects the host is acquired not only by the contraction of the period of egg-laying but also by the rationing of the latter. In separate cases, this apportioning of the egg-laying is carried out differently.
Thus we saw that among a number of worms this is linked with the simultaneous deposition of eggs joined by filaments, or little feet and filaments, to each other (a number of Microcotyle and others, see page 90), or with the speed of deposition at a determined time of the day or determined conditions of the external medium (many lowest forms--Dactylogyridae and others). Finally, among P. integerrimum the apportioning of the deposition of eggs is connected with the peculiarities of life activity of the host, because the eggs are ejected in large numbers periodically during the emptying of the urinary bladder of the frogs.[1]

The shortening of the period of formation and deposition of eggs creates a necessity of a large number of morphophysiological peculiarities in the functioning of the sex system. As we saw in the example of *P. integerrimum* from the urinary bladder, the yearly cycle of the sex system is completely subjugated to this problem and the processes of oögenesis and spermatogenesis, of the formation of vitelline food cells, the production of all auxiliary glands becomes strictly cyclical and takes place in such a fashion as to make possible the maximal use of all sex products which are available in the shortest period of the egg-laying. This is especially noticeable in comparing the characteristics of action of the sex system and the morphological peculiarities in both forms of *P. integerrimum*. We will note once more that "gill" *P. integerrimum* with an extended (although relatively short in time) period of the action of the sex system do not have a uterus but only an oötype, they have a different form of the ovary connected with a gradual ripening and expenditure of egg cells, and they have no vaginal ducts, etc. The differences in the deposition of eggs of both forms are closely related to the peculiarities of life and location of the stages of development of frogs infected by them. *P. integerrimum* from the urinary bladder has the opportunity of depositing eggs under conditions favorable to the subsequent development of the larvae only during the short period of the presence of the frogs in the body of the water at the time of their spawning p. 130 because at another period the frogs are located in a different medium of habitat, and the eggs of the parasite deposited at the time are inevitably condemned to death. The gill form of *P. integerrimum* parasitizes tadpoles for its entire life and perishes with their metamorphosis, consequently eggs deposited by it during the entire period of egg-laying fall into the medium favorable for the development and, as we saw before, have considerable chances for infecting the host. Along with the changes in the structure and functioning of the sex system, a number of adaptations toward peculiarities of life cycle is reflected in the structure of the eggs and also in the place of their location after deposition, as was previously mentioned. The retention of eggs on the body of the host is an important adaptation among many forms parasitizing fishes which lead a gregarious form of life and which perform considerable migrations. Among parasites of such fishes, it gives the same result as rationed egg-laying, as was already noted. However, here we encounter the substantial question of cross-infection of the fishes for without the latter the probability of the flourishing of the parasites as a species would have been extremely small. Increased infection of the same individual of host by newer and newer individuals would have worsened the conditions of existence of the host and by that very fact would have influenced negatively the condition of the existence of the parasite

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[1] Indications to the effect that at the time of deposition, *P. integerrimum* extends outside from the cloaca are not substantiated by our observations.

itself. As was already indicated (see page 93), we clearly differentiate two periods in the life of the free-swimming larva: non-invasional, when the larva is still not in condition to infect the host; and invasional (there is still another non-invasional period when the larva already is not in a condition to infect the host and thus is condemned to perish). The first of these enumerated periods is of special and extremely important significance because it enables the larvae emerging from the egg which is located on the host individual to infect another individual. In addition to the presence of morphological peculiarities, this is accomplished by the action of a positive phototaxis which has a direct significance in the dissemination of the larvae, whereas the relative speed of their mobility creates the possibility of a sufficient eloignment (separation, *nobis*) of the host on which the parent individual was located. The periods of development of the egg which undoubtedly also have adaptive significance are also closely connected not only with the internal peculiarities but also the external ones, and in the first order primarily with the temperature factor. This is clearly apparent in the case of "winter" eggs of *Dactylogyrus vastator* Nybelin and in the case of the coincidence of the periods of development of the eggs of *P. integerrimum* with the time of the development of roe and the larvae of the frogs which also depends on temperature.

The historical process of the adaptation of the life cycle of the parasitic monogenetic trematodes to the peculiarities of life of their hosts proceeds along the line of limiting the possibilities of infecting unusual hosts or unsuitable stages of the life cycle of the host and leads in a number of cases to the development of a very narrow specificity in the true sense of the word. However, the life cycle of monogenetic trematodes reveals to us also a number of other methods of limiting in time and space the possibility of infecting hosts during less suitable stages of their existence, while preserving the potential capabilities toward infecting any stages and even other types of hosts. This extremely important peculiarity is of tremendous biological significance. This question will be analyzed in detail in the chapter concerning specificity and incidence of occurrence of Monogenoidea (see pages 283-299).

In the process of adapting to the infection of the host during the specific stages of its life we see two basic tendencies, the first of them leads to the development of adaptations toward infection and conditioning p. 131
the entire life cycle of the parasite to the younger ages of the host as takes place for instance among *Protancyrocephalus strelkowi* Bychowsky and the second leads to the ability of normal infection of the host, basically in its younger stages but after the parasite has reached maturity on adult individuals. Apparently both tendencies are connected not only with the peculiarities of the embryology of the host but also with the degree of advancement of organization of the parasites and the duration of their lives. As a rule the first tendency is observed among the lowest and the second among the highest of monogenetic trematodes. When we speak about young stages

of the host we mean, in the majority of cases, individuals up to two years old among polyannual hosts or even younger among quickly-maturing and growing fishes; however, one must bear in mind that for each type of host of egg-depositing Monogenoidea there is a proper period before which it (the host, *nobis*) is not infected. The reasons for this are not clear and it is possible that they are hidden in the morphological peculiarities of the gill apparatus which the large mass of monogenetic trematodes parasitize. N. A. Izumova, who was interested in this question, established that among *Dactylogyrus vastator* the infection of young carp is possible only when they reach the sizes from 10 to 12 millimeters and she came to the conclusion that this stands in direct relation to the degree of morphological differentiation of the gill apparatus of the fishes.

The representatives of the viviparous family Gyrodactylidae have a special type of life cycle. Its basic peculiarity appears to be the absence of a special morphological differentiating stage which serves for the infection of the new individuals of the host. The infection, as we succeeded in establishing in special studies, takes place by fully mature parasites which transfer from one host individual to another when they come close to each other. One must say, however, that as yet much remains unclear because the reasons causing the worms to leave the host are not fully understood, for we never observe direct contact between fishes in normal conditions, even among the majority of gregarious forms. Consequently, the worms and especially those which are located as a rule on the gills must make special effort to come out of them and actively try to transfer to another host. We hope that further experimental research will clarify this interesting question. The life cycle of *Gyrodactylus* has apparently a relatively simple character. Multiplication of worms takes place during the entire summer period and apparently more or less evenly all the time. The daughter individual is born when it is already fully formed and does not differ from the mother individual either in structure or in size (Fig. 131). Based on our observations of *Gyrodactylus* sp. sp. from the Stickleback, in the mother individual, after a rather short period of time following the birth, a new egg enters the uterus and begins to cleave and the process of its development until birth of the new daughter individual lasts normally about 4 to 5 days. The number of births in one mother individual has not been exactly ascertained, but according to the indirect evidence it is not less than 3 to 4. We happened to observe that after one of the births of the daughter individuals the mother individual almost immediately perishes, whereas in other instances the mother individual after a certain period of depression becomes normal, beginning to feed and to move actively. Thus, according to all observations the life span of a particular individual *Gyrodactylus* lasts not less than 12 to 15 days and possibly even considerably longer. The fate of the daughter individual is somewhat different than the mother individual, for after the birth it has already in the uterus a strongly developed p. 132
embryo which is born approximately a day later and which in turn contains an embryo in the uterus. Since up to four embryos usually result from one

egg, as was indicated before, we obtain four unequal individuals following their birth. Thus, the first born individual has in its uterus three embryos lying one inside the other, the second--two, the third--one embryo, and the fourth--none. In such a fashion the first three daughter individuals differ from the fourth by the fact that up to the beginning of the development of the embryo formed from its own egg they must give birth to one "remaining" embryo from the same egg cell as they themselves are. In contrast to them the fourth individual begins to give birth only to embryos resulting from its own eggs. This difference exists in each generation of *Gyrodactylus* and in such a fashion each individual has differences within the first period of its existence.

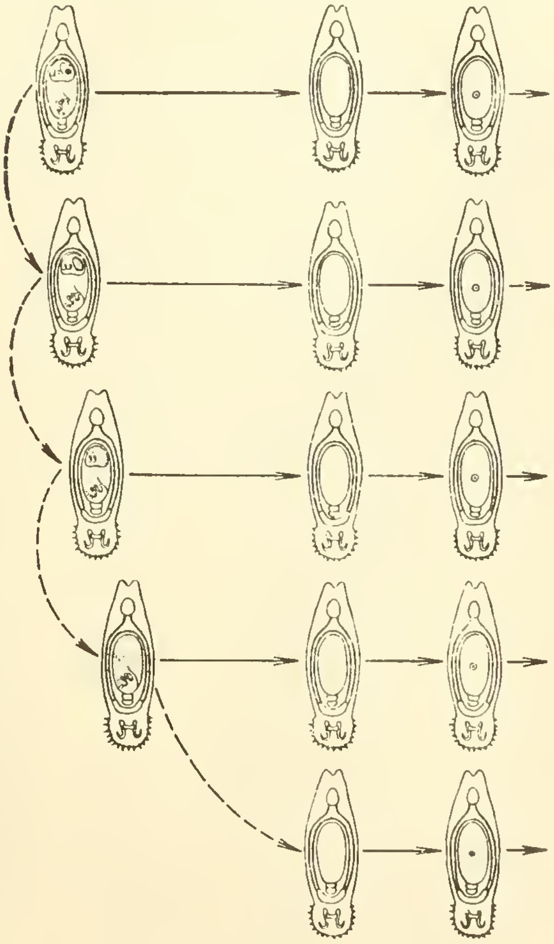

Fig. 131. *Gyrodactylus rarus* Wegener, diagram of reproduction. The birth of a new individual is represented by the interrupted line, the continuous line represents life of the separate individual. The last born embryo is darkened. Among worms which "gave birth" to a young individual the uterus is conditionally indicated in inflated form (middle row) just as among worms which still have an uncleaved egg in the uterus (right row); in nature after "giving birth" to the young individual, the uterus of the mother individual strongly deflates.

From the observation on the incidence of different types of *Gyrodactylus* it is possible to conclude that here also the cycles differ considerably. Thus, certain types are encountered only on young individuals of the fishes and are always or almost always completely absent in the older ones [for instance, *G. proximus* Bychowsky and Poljansky from *Pallasina barbata* (Steindachner)] and on the other hand, other types are discovered mainly on groups of older stages of the host [*G. marinus* Bychowsky and Poljansky from Cod and Minitia (or Pollack, *Theregra chalcogramona*, *nobis*)]. Just as among the egg-depositing forms, among *Gyrodactylus* there are some that are encountered only on inshore fishes [*G. perlucidus* Bychowsky and Poljansky from the Beldug (Ling or Quab, *nobis*)] and on fishes which live far from the shore in the upper layers (*G. pterigialis* Bychowsky p. 133
and Poljansky from the Pollack) or in relatively great depths (*G. colnephori* Bogolepova from *Comephorus dybowskii* Corotneff). Finally certain species live on gregarious fishes (*G. bychowskyi* Sproston from

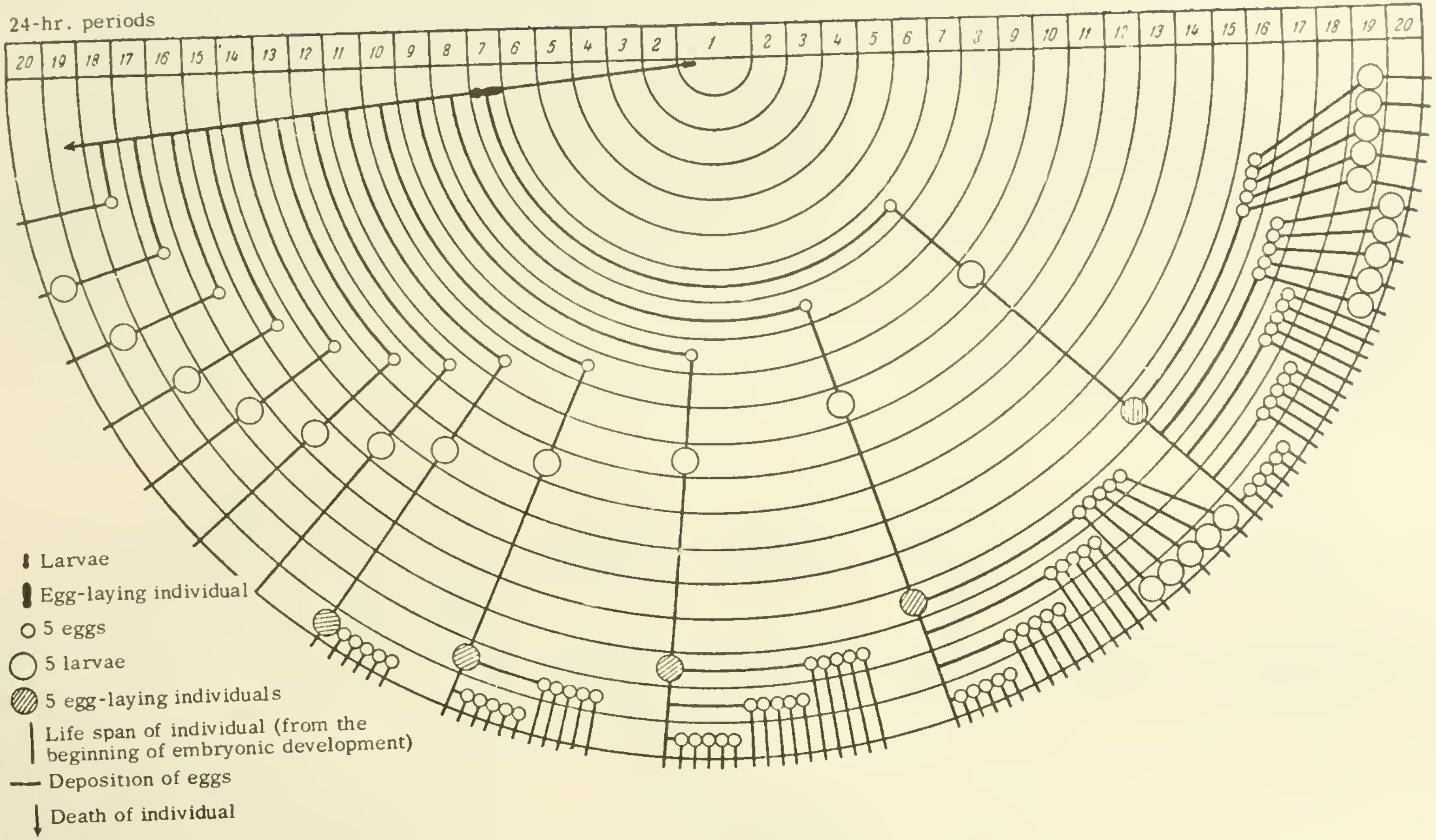
24-hr. periods
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Larvae
Egg-laying individual
5 eggs
5 larvae
5 egg-laying individuals
Life span of individual (from the beginning of embryonic development)
Deposition of eggs
Death of individual

Fig. 132. Diagram of spawning and of the number of progeny of one individual of Dactylogyrus during the period of 20 days.

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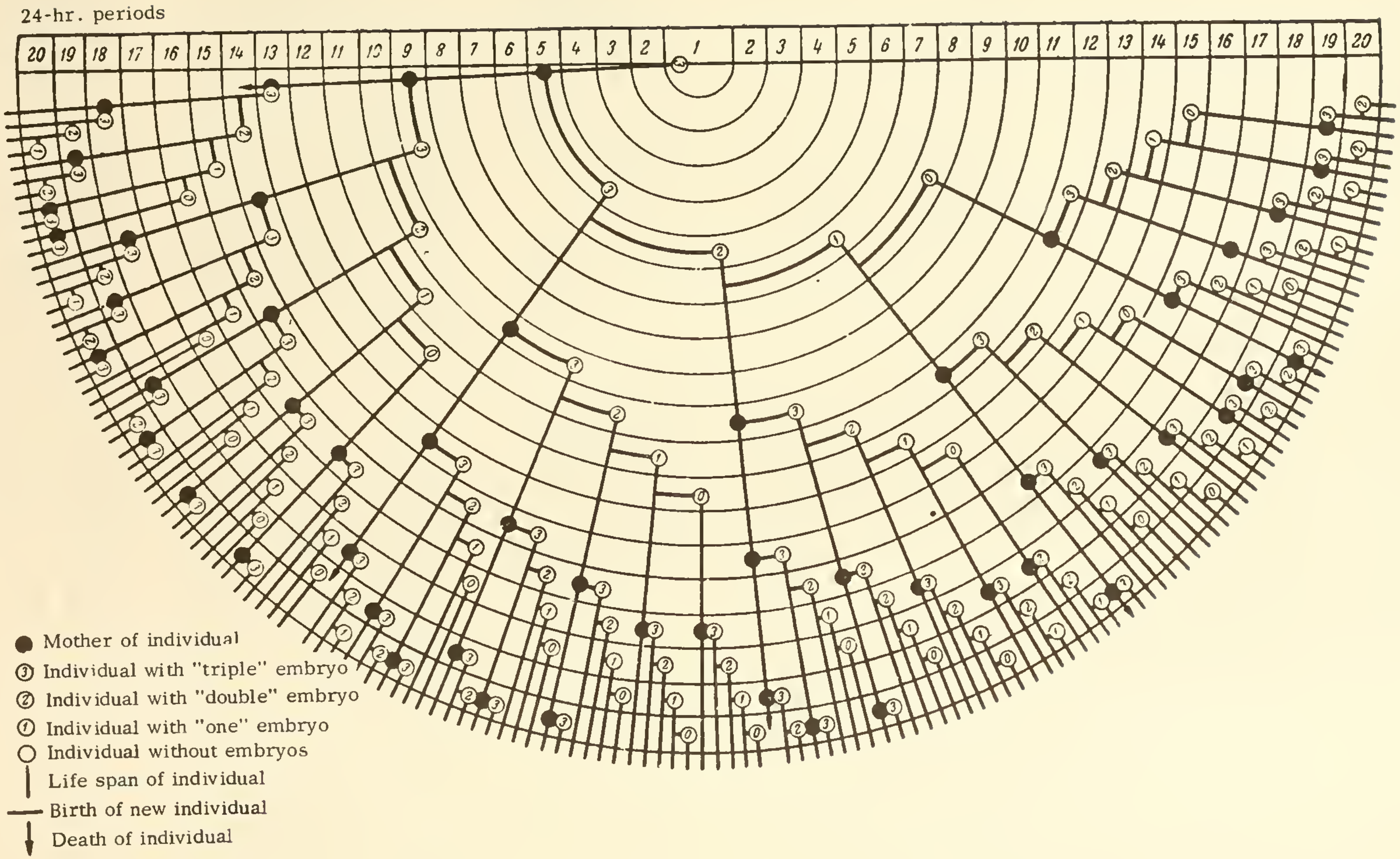
24-hr. periods
20 19 18 17 16 15 14 13 12 11 10 9 8 7 6 5 4 3 2 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
● Mother of individual
③ Individual with "triple" embryo
② Individual with "double" embryo
① Individual with "one" embryo
○ Individual without embryos
Life span of individual
Birth of new individual
Death of individual

Fig. 133. Diagram of accretion in numbers of progeny of one individual of Gyrodactylus during 20 days.

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stickelbacks) and others on solitary fishes (G. groenlandicus Levinsen from gobies). All this taken together means that the question concerning life cycles of different Gyrodactylus deserves special studies and probably will yield much that is new and interesting.

In connection with the problem of life cycles, one must pause to examine certain aspects of the question of dynamics of numbers of monogenetic trematodes. As we have already indicated (page 80), this question has great practical significance in addition to the theoretical one. First of all let us analyze the peculiarities of accretion in numbers under ideal conditions for egg-depositing and viviparous forms. As examples for the analysis of the given phenomena it is convenient to use the material on Dactylogyrus vastator Nybelin and Gyrodactylus elegans Nordmann from Carp. We shall attempt to show in which fashion the numbers must accrue among both types, on the condition that all the larval Dactylogyrus emerging from the eggs, or correspondingly all the individuals of Gyrodactylus which are born, survive and continue their normal existence until natural death from old age. It is understandable that this almost never occurs in nature, but such a theoretical calculation will give us much that is essential for the understanding of relations between both types of reproduction. For the estimate of the reproduction of D. vastator we take the following data (see page 108): the period of development of eggs--three days, development of larvae until maturity and first deposition of eggs--6 days, the span of life from the moment of maturity--12 days, the number of eggs deposited daily--5; for G. elegans (see page 131): the development of eggs in the uterus until the emergence of the first daughter individual--4 days, the emergence of "remaining" embryos in sequence a day after the birth of the corresponding worm, the span of life of the worm from 13 to 14 days depending on the presence or absence of "remaining" embryos. Of course, all these periods are inexact and can have only an orienting significance. For practical purposes the calculation of the accretion of numbers of both types within the limits of one month is interesting because this is the usual period of crowding of the young fishes in the spawning ponds where greatest infection is possible and where occurrences of epizootics are even observed. The common scheme of accretion of the progeny from one individual D. vastator and G. elegans is represented in Figs. 132 and 133. They are compared in such a way as to make the general character of changes apparent. Unfortunately, technical difficulties permitted us to represent the process for only 20 days. As for the remaining period the development of changes is expressed in curves of the accretion of numbers (Fig. 134 and Table 2).

From these data it is apparent that the resulting figures of the changes in numbers of both types obtained almost coincide basically in spite of the completely different means of reproduction. Moreover, Gyrodactylus yields a greater number of progeny during the first period (up to 20 days) than Dactylogyrus. The first interesting deduction from this is that viviparous Gyrodactylus potentially possess a very high tempo of reproduction which is not inferior to the species which reproduce by means of egg deposition, which at first glance may seem completely improbable because it is commonly accepted that viviparousness is linked with a decrease in the numbers of the progeny with the better insurance of survival. The second deduction from what has been said is that epidemic outbreaks which are observed in carp industries can be easily explained even with the presence of a weak infection in the producers which are the initial source of the infection p. 136 of the young ones. Finally the third conclusion from these theoretical calculations is that the most desirable conditions in the carp industries is the most rapid transfer of young fishes from the spawning ponds into the growing ponds which completely coincides with direct observations on the dynamics of the numbers of *Dactylogyrus* and *Gyrodactylus* in natural conditions.

One must say that the calculations cited and the discussion about the ideal quantity of *Dactylogyrus* and *Gyrodactylus*, even though they explain certain phenomena observed in carp industries under considerable crowding of hosts, are nevertheless far from what exist in natural conditions. Actually the quantity of individuals depends not only on the productivity of the worms but also on a great number of external factors which, in a great majority of cases, determine the quantity of parasites. This also applies in considerable measure to the carp industries,but it is more strongly expressed in nature.

At the head of the factors which greatly influence the quantity of monogenetic trematodes, one must place the means of infection, the temperature regime of the surrounding medium, the correlations between the place of deposition among the egg-depositing forms with the place of the most frequent presence (occurrence, *nobis*) of the schools of the hosts and the frequency of their populations,and so forth.

It is interesting to note that the question about the methods of infection of the hosts of *Gyrodactylus* cannot be considered as completely solved even at the present time. As was already pointed out the representatives of this genus apparently have different life cycles,and at the same time one must consider tentatively the considerable differences between the theoretical accretion of numbers of the worms and the one which is observed in nature, as a rule, where a large number of *Gyrodactylus* on the body of the host, even in conditions of spawning ponds of the carp industry, is an exception. Consequently, the infection by these worms has certain peculiarities which prevent the survival of the majority of born individuals. Whether this is a result of the complexity of the infection of the fishes by means of adult worms or whether some other factors play a role here so far is unknown.

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In conclusion let us note that the problem of dynamics of numbers of Gyrodactylus still demands considerable work for its successful solution. Without it, it is not possible to utilize fruitfully the data about life cycles for the purpose of preventing parasitic infections.

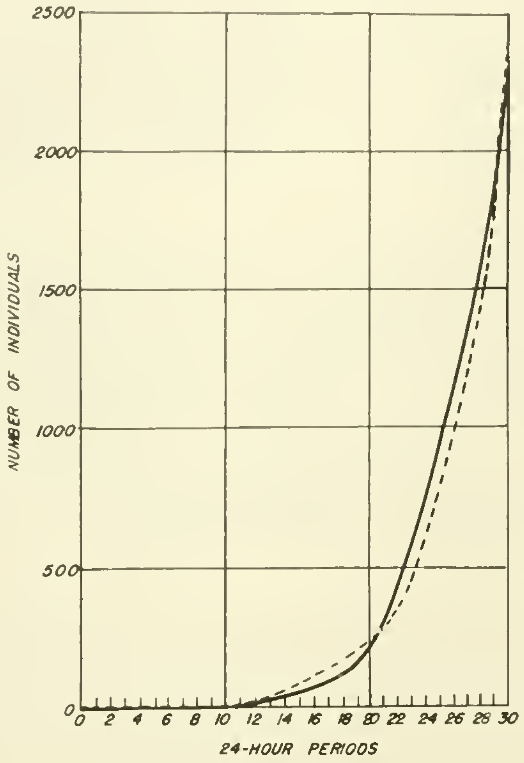

Fig. 134. Accretion curves represent numbers of the progeny of individual Dactylogyrus and Gyrodactylus. 1-Gyrodactylus; 2-Dactylogyrus.

TABLE 2

Accretion in number of individuals *Dactylogyrus vastator* Nybelin and *Gyrodactylus elegans* Nordmann, obtained from one initial sample of each type (theoretical estimate).

24-hour period	Number of individuals *D. vastator*	Number of individuals *G. elegans*	24-hour period	Number of individuals *D. vastator*	Number of individuals *G. elegans*
1	1	1[1]	16	36	46
2	1	1	17	41	62
3	1	1	18	46	82
4	1	1	19	75	109
5	1	2	20	130	142
6	1	3	21	210	190
7	1	4	22	310	253
8	1	5	23	435	338
9	1	6	24	585	446
10	6	8	25	760	590
11	11	11	26	960	784
12	16	16	27	1185	1053
13	21	20	28	1555	1398
14	26	26	29	1950	1851
15	31	34	30	2320	2452[2]

[1] Beginning of the deposition of *D. vastator* and the formation of the first egg of *G. elegans*.

[2] In *D. vastator* 570 are mature and the rest are young. All *G. elegans* are with embryos.

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DATA ON THE DEVELOPMENT OF MONOGENETIC TREMATODES

Below is expressed all the information at our disposal on the development of separate species and genera of monogenetic trematodes from literature as well as that based on our studies. The main attention is directed to the structure of the larvae and the development of chitinous elements of the attaching disc which have, as has already been indicated, important significance in the systematics of the group. The data on the development of separate species are preceded by short descriptions of the structure of adult animals which aids the understanding of the peculiarities of development. The data on the development of the viviparous genus Gyrodactylus Nordm. are not included (see page 92). p. 138

1. The development of Acolpenteron, Fischthal and Allison

In 1940, Fischthal and Allison (Fischthal and Allison) described Acolpenteron ureteroecetes--a new genus and species of the simply organized monogenetic trematodes parasitizing the ureters of fresh water fishes of North America. A year later they also described the second species of the genus A. catostomi and gave succinct data on its development adding a drawing of the free-swimming larva. The adult Acolpenteron (Fig. 44) has an attaching disc which is weakly-delineated from the rest of the body. It is equipped with 14 edge hooks of the type usual for Dactylogyridae with the widened part of the upper handle. There is no other armature on this disc besides these hooks. E. V. Gvozdev (1945), who described a third type from Kazak SSR (regions surrounding Alma-Ata) indicates that worms of this species are located freely in the lumen of the ureters. The absence of pigmented little eyes is characteristic for representatives of this genus, more precisely their degeneration, for on the anterior end of the body in front of the pharynx there is a considerable number of pigmented seeds lying in scattered fashion in the parenchyma. The anterior end of the body with two weakly expressed head growths, with the sensitive hairs (?) and with the ducts of the head glands opening into these growths. The digestive system has a rounded pharynx and two straight intestinal trunks merging at the posterior end of the body. The sex complex lies at the center of the body between the intestinal trunks. The eggs of A. catostomi (Fig. 135) are deposited in the ureters of the host and are discharged with the urine into the water and develop on the bottom. The authors indicate that cleavage takes place only after the eggs reach the water and that all the embryonic development takes place within 6-9 days. At the end of this period a free-swimming larva (Fig. 136) emerges from the egg. This larva is 0.123 millimeters long and 0.040 mm wide, and is equipped with ciliary p. 139
epithelium located in four groups of cells. One of these groups is located

on the anterior end of the body of the larva, two on its sides, the right and the left, somewhat behind the pharynx, and finally the last group lies on the posterior end of the body. The larva has two pairs of well-developed pigmented little eyes lying in front of the pharynx. The little eyes are equipped with light-refracting lenses located laterally. The little eyes of the anterior pair are 0.006 mm in diameter, whereas the sizes of the posterior--0.008 x 0.010 mm. Very frail edge hooks, about 0.019 mm in length, are located on the cup-shaped (?) attaching disc. Their number is 14, just as among the adults.

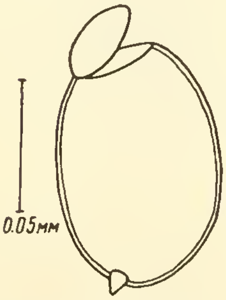

Fig. 135. *Acolpenteron catostomi* Fischthal and Allison, egg. (According to Fischthal and Allison, 1941.)

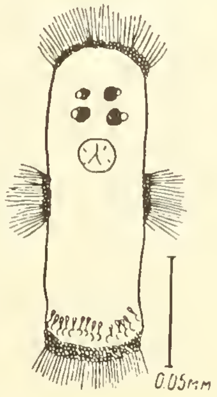

Fig. 136. *Acolpenteron catostomi* Fischthal and Allison, free-swimming larva. (According to Fischthal and Allison, 1941.)

Further development is not described but is sufficiently evident.

2. Development of *Dactylogyrus* Diesing

The development of the worms of the genus *Dactylogyrus* was studied by a number of authors. The first data on the biology of the development and reproduction of eggs with the developing larvae of *D. vastator* Nybelin were given by Nybelin in his work of 1925. Later, in two of her works, Kulwiec (Kulwiec, 1927, 1929) describes the development of *D. anchoratus* (Dujardin), *D. crassus* Kulwiec and *D. vastator* Nybelin, separate stages of development of *D. formosus* Kulwiec and *D. wegneri*

Kulwiec and adds figures of the free-swimming larvae of D. crassus
Kulweic and D. vastator Nybelin. Wilde (Wilde, 1937) gave a description
and a number of figures of the development of D. macrocanthus Wegener
and in 1940 Groben (Groben) cites an analogous research to her work on
D. vastator Nybelin and partially on D. anchoratus (Dujardin) and D.
macrocanthus Wegener. Certain material on the development of D.
vastator Nybelin and D. solidus Ackmerow is given in the works of E. M.
Lyman (1939 - 1951) and O. N. Bauer (1948 - 1953). A collaborator of our
laboratory A. V. Gussew in 1949 - 1950, who studied monogenetic trema-
todes of Lake Hanka, secured during the course of his works certain
material on the development of 9 species of Dactylogyrus: D. curvicirrus,
Achmerow; D. gussevi Achmerow, D. phoxini Malewizkaja, D. eryth- p. 140
oculteris Gussew, D. achmerowianus Gussew, D. contortus Gussew,
D. obscurus Gussew, D. peltatus Gussew and D. leucisculus Gussew.
Finally during the period of 1927 - 1949 we studied the development of
13 species D. anchoratus (Dujardin), D. intermedius Wegener, D. vastator
Nybelin, D. wegeneri Kulwiec, D. formosus Kulwiec, D. cornu Linstow,
D. fallax Wegener, D. crucifer Wegener, D. longicopula Bychowsky, D.
solidus Achmerow, D. varicorhini Bychowsky, D. pulcher Bychowsky and
D. modestus Bychowsky, with a varying degree of completeness.

The adult Dactylogyrus (Fig. 5) is characterized by more or less well-delineated attaching discs equipped with 14 edge hooks of approximately the same type as Acolpenteron and two middle hooks between which lies a chitinous connecting plate. In approximately half of the species of this genus there is, in addition, a supplementary chitinous plate located between the middle hooks also but not directly connected with them, which apparently serves for the attachment of musculature and the mechanical fastening of the disc. The anterior end of the worms has four head growths and two pairs of well-developed pigmented little eyes. The digestive system consists of a powerful pharynx and smooth intestinal trunks which merge at the posterior end of the body. It forms in such a fashion an ellipsis inside of which the sex system lies. A powerful development of chitinous elements of the copulatory apparatus is characteristic for this genus and has important significance in systematics. For the most part the eggs of Dactylogyrus (Fig. 137) are deposited to the bottom although samples may delay themselves on the gills of the host.

In normal conditions, embryonic development lasts from 2-1/2 to 10 days depending upon the temperature of the water which surrounds the egg (see page 92). The larva which has just emerged from the egg has a length generally 1-1/2 times larger than the length of the egg. For instance, in D. wegeneri Kulwiec the length of the egg is about 0.070 mm, whereas the length of the larva is about 0.100 mm, correspondingly among D. vastator Nybelin 0.090 and 0.125 mm and D. macracanthus Wegener--0.075 and 0.120 mm. The length of the larva in relation to the length of the body of the adult worm varies greatly and the relationship between them p. 141

can fluctuate considerably. For instance, in D. wegeneri Kulwiec this ratio is approximately 1 to 5 and in D. vastator Nybelin 1 to 9, i.e., almost twice as long.

The larva which has just emerged from the egg swims freely (Fig. 138). It is covered with ciliary epithelium located in three zones just as in Acolpenteron. The first zone, consisting of two groups of ciliary epithelium, lies at the anterior end of the body and extends posteriorly approximately to the level of the posterior pair of eyes. Each of the groups is located laterally, extending, however, to the ventral and dorsal sides of the body, but they come in contact only at the anterior end during its contraction.

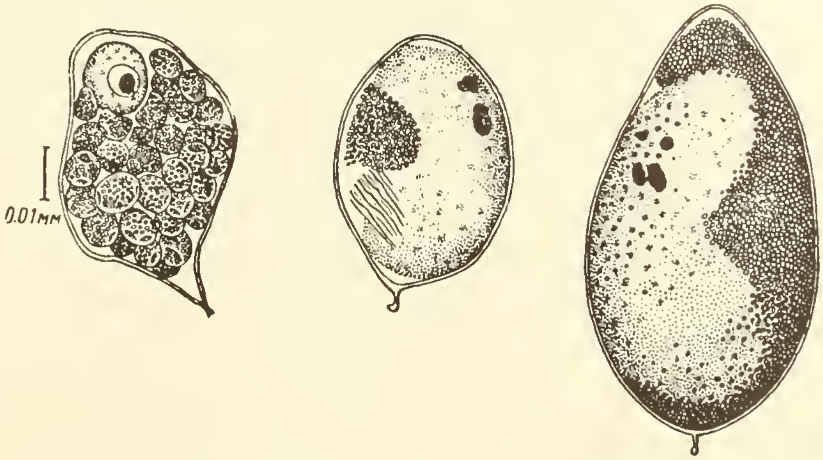

Fig. 137. Dactylogyrus vastator Nybelin, left egg is separated from the uterus of the worm and has not yet been completely formed; the two remaining eggs with developing larvae were deposited by one individual. (According to Bychowsky 1933).

The second zone lies behind the pharynx approximately in the middle of the body and its posterior edge is located at the level of the upper ends of the edge hooks. This zone consists of two groups of epithelium located along the sides of the body. The third zone of ciliary epithelium lies at the extreme posterior end of the body of the larva and apparently originates from two groups of cells (Kulwiec, 1927, Table 21, Fig. 2) mostly fused together. It is somewhat displaced to the dorsal side and is located on a special growth of the body which is very mobile and which disappears later. During attempts to count the number of ciliary cells, it was possible to determine that in D. intermedius it is relatively large (compare with Polystoma, page 182); thus, in the anterior zone there are more than 18 ciliary cells. At first the body of the free-swimming larva is elongated in the shape of a cigar, its attaching disc is not differentiated and has a common contour with the body representing its direct and gradually narrowing end. The internal organization of the larva resembles that of the adult worms, its anterior end is equipped with two growths into which head glands open. At first these growths are only weakly noticeable. Two pairs of pigmented little eyes of very large size are located between them and the pharynx. The posterior pair is larger than the anterior and is equipped with larger light-refracting lenses. There are weakly developed nervous and excretory systems. The digestive system is represented by a well-developed small pharynx and in relation to the size of the pharynx, a disproportionately small intestine which has the appearance of a ring. The chitinous armature of the attaching disc is represented by very frail small edge hooks, the number of which is the same as among the adult forms. These edge hooks which as yet do not have the final shape are located p. 142 in the posterior part of the body and lie there in groups which are more or less parallel to the axis of the body of the larva, motionless and not extending outside. After a certain interval of time, somewhat before the finding of the host, considerable changes take place in the behavior and structure of the larva. The larva which has just emerged from the egg possesses a positive phototaxis which later changes to negative. The attaching disc of the larva begins to delineate itself, acquires the typical form and relationship to the body; it stands at a certain angle to the body, becomes round and at that time is much thinner than the rest of the body. At the same time, the edge hooks, so to speak, descend toward the edges of the discs and occupy their final places, they cut through to the outside terminally and at times begin to move in a lively fashion. The larva begins to stop near different underwater objects as if feeling them with its anterior end (at that time the head lobes are already distinctly visible), it often contracts and attempts to attach itself. This period normally terminates in the larva finding its host and attaching itself to its gills, fins or skin. When it does not find a host, it descends to the bottom and perishes rather quickly. Among representatives of the genus, the period of the free-swimming larva extends from 4 to 20 hours and the period during which the larva is capable of infecting a host is considerably shorter--does not exceed 5 hours.

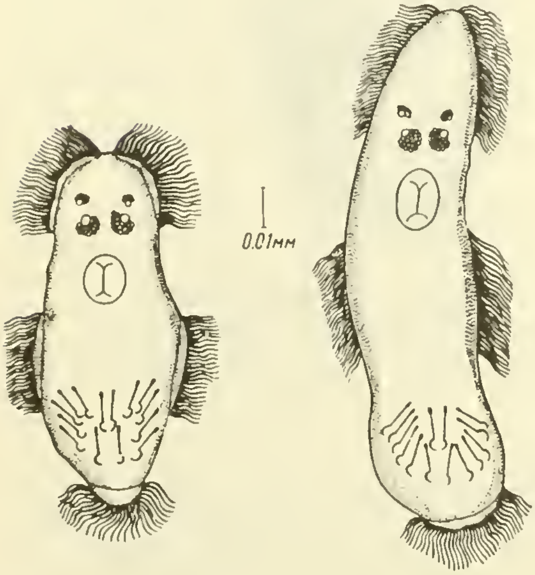

Fig. 138. Dactylogyrus vastator Nybelin, larvae in different stages of contraction.

After attaching itself to the body of its host the larva throws off the ciliary covering and begins to feed and grow at an accelerated rate. During the growth of the body and parallel to it, takes place the growth of the nervous, the excretory, and the digestive systems which gradually acquire their final form. Very quickly after the attachment, the two head growths are supplemented by two more and the head end also acquires its final structure. The eyes of Dactylogyrus either do not grow at all from the moment of emergence from the egg, or if they grow they do so very slowly. Among many forms the eyes degenerate, dividing into separate pigmented granules which remain near the anterior edge of the pharynx during the entire life.

The development of the attaching apparatus deserves undivided attention. The edge hooks of the free-swimming larva (Fig. 139) have an already well-expressed division into two parts: the terminal little hook and the handle. The terminal little hook of the edge hook distinguishes itself from that of the adult form only by somewhat more general outlines and thickness (at first among a number of species it somewhat thickens proportionately to the growth of the entire edge hook); the handle of the little edge hook is in the shape of a little stick, sometimes with a small widening at the free end. When this widening occurs, its length (from the terminal hook to this widening) corresponds to the length of the basal part of the handle of a fully-developed edge hook. Subsequent growth of the handle takes place by way of the accretion of newer parts onto its free end until the lateral hook reaches the final dimension and form. The stem of the larval edge hook somewhat thickens during the time of its subsequent development just as in the terminal little hooks. The tempo of growth of the edge hooks among different types of Dactylogyrus varies and the development of hooks of separate pairs takes place unequally: some of p. 143 them reach larger sizes and have sometimes somewhat different shapes then others (Fig. 140). For the most part, the second, third and fourth pairs acquire larger sizes, whereas the sixth and seventh are the smallest. In such a fashion, the accretion of new parts while preserving shapes and linear measurements of those already existing is characteristic for the development of the edge hooks. This phenomenon is so typical it is almost always possible to indicate with a great degree of precision the sizes of the hooks of the free-swimming larva from the sizes of the edge hooks of the adult animal. One must note that the development of edge hooks of D. anchoratus (Dujardin) is described quite correctly in the work of Kulwiec (1927), whereas the figures of the development of edge hooks of this species and also of D. vastator Nybelin and D. macrocanthus Wegener

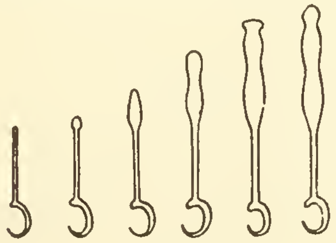

Fig. 139. The diagram of the development of edge hooks in Dactylogyrus.

by Grobin (Grobin 1940) are completely inaccurate.

The middle hooks (Fig. 141 and 142) are incepted already after the attachment of the larva and its growth to a certain size, and in the beginning they are located not in the attáching disc but somewhat in front of it in the parenchyma of the posterior part of the body, and only later do they descend into the disc. At the earliest stage of development of the middle hooks they have the appearance of two almost parallel threads of more or less equal thickness, with somewhat sharpened lower ends (corresponding to the point of the fully developed middle hook) and with the upper end slightly curved toward the middle of the body of the larva. Just as among edge hooks its further development takes place by means of certain thickening of the existing parts and mainly by way of the accretion on the upper end, at first on the base of the hook, and then at both extensions. During this, in a number of cases, no changes in form take place in the existing parts, in other cases during the early stages p. 144
(until the beginning of its functioning), the hook is somewhat straightened in comparison with its normal form and bends only during the period of growth of the second half of its base part. The inception of the connecting plate already takes place (Fig. 143) at the time when the middle hooks occupy the final position on the attaching disc but are still in the early

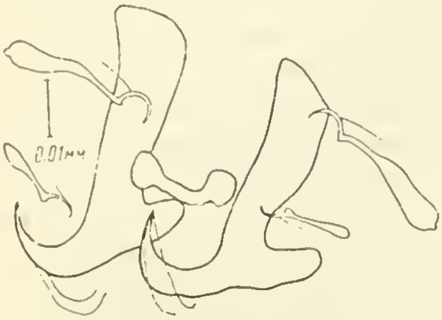

Fig. 140. Dactylogyrus similis Wegener, attaching apparatus of a disc of an adult individual from the gills of Leuciscus leuciscus (L.) from the Gulf of Finland near Peterhof. Sixth and seventh pairs of edge hooks are (sizes and shapes!) represented in addition to the middle ones.

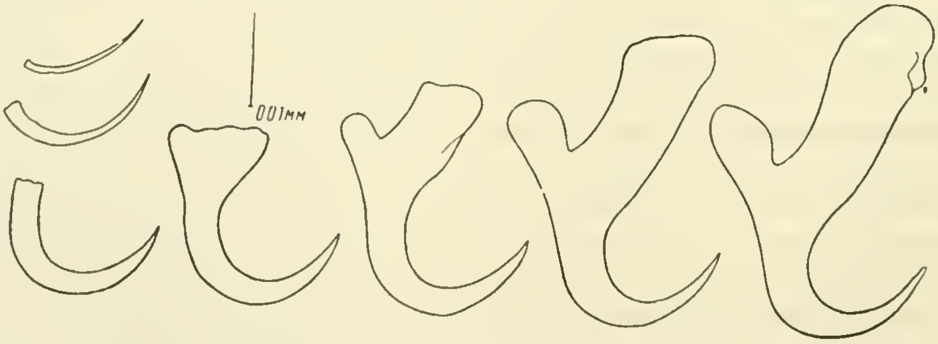

Fig. 141. Dactylogyrus alatus Linstow the development of middle hooks of the disc of the worms from the gills of Alburnus alburnus from the Delta of the Volga.

stages of development (on the average apparently before the appearance of the second half of the base section). This plate is incepted in the shape of a thread curved transversly and grows in length as well as in width. Among different species its development is somewhat different: in some it simply reaches its final shape and size gradually, as for instance among D. anchoratus (Dujardin) and among others it first curves in the middle depending upon its final shape, for instance D. longicopula Bychowsky (Fig. 144).

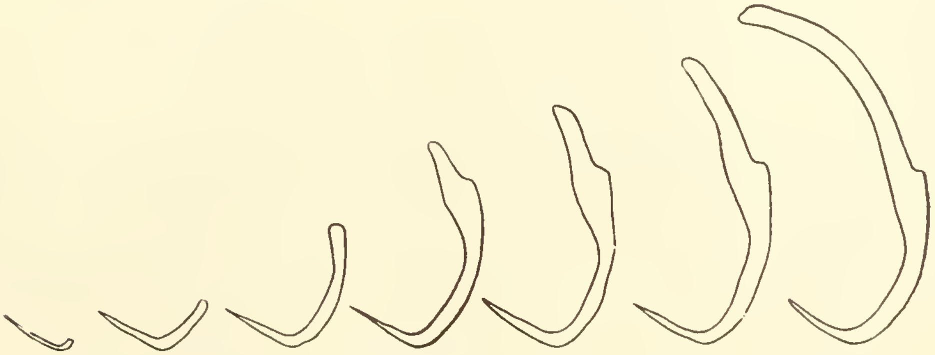

Fig. 142. Dactylogyrus anchoratus (Dujardin),development of middle hooks of the disc. Enlarged 375 times. (According to Kulwiec, 1927).

This terminates the development of the attaching apparatus among the group of Dactylogyrus which lacks a supplementary plate.

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[1] In the development of worms of this group, Kulwiec (Kulwiec, 1927) distinguishes three stages (four, to be exact, because she subdivided her second stage into two periods). As her research correctly indicates, these stages are artificial but very convenient in the determination of development and comparison of the tempo of development among different species. The signs which differentiate the stages are: first stage--the larva (which has lost its ciliary epithelium and begun to grow) until the appearance of the inceptions of the middle hooks; the first part of the second stage is characterized by the appearance of the middle hooks and extends until the inception of the connecting plate; the second period of this stage begins from this moment and terminates at the beginning of the third stage which starts from the appearance of the interior excrescences of middle hooks.

The supplementary plate, which exists in the second group of Dactylogyrus appears as the most variable part of the attaching armature in shape as well as in size (in relation to the rest of the armature) (Fig. 145). Among adult Dactylogyrus one can observe the supplementary plate in the shape of a simple transversely elongated stick, in the shape of a triangle, in the form of a T or inverted T of more complex form. Thus, for instance, in the group of *D. kulwieci* Bychowsky the supplementary plate consists, as it were, of two halves connected by a small membrane and the part which faces the lower edge of the disc has the shape of an inverted fleur-de-lis, whereas the upper one is bent in the shape of a V or U. As an exception, there exist connecting plates elongated longitudinally in the shape of a stick, as for instance among *D. simplicimalleata* Bychowsky. In spite of all the different forms of the supplementary plates, p. 145 one can establish on the basis of the observation of their development that these are homologous formations,[1] the evolutionary development of which takes place in a completely determined fashion. The supplementary plate

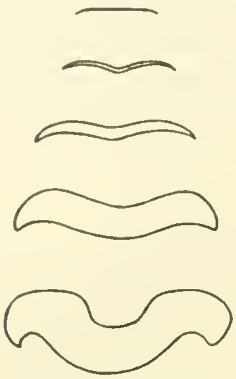

Fig. 143. Diagram of the development of the middle plate of *Dactylogyrus*.

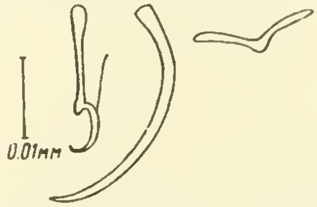

Fig. 144. *Dactylogyrus longicopula* Bychowsky, attaching armature of a young worm in the process of development from the gills of *Schizothorax intermedius* McCl. from the river Varzob (Tadjikistan, SSR).

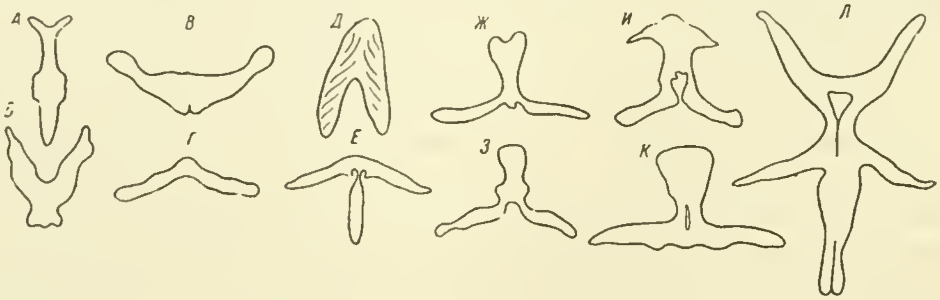

Fig. 145. The shape of the supplementary plates of the attaching discs of various species of *Dactylogyrus*. A—*D. simplicimalleata* Bychowsky; B—*D. bicornis* Malewitzkaja; C—*D. cryptomeres* Bychowsky; D—*D. alatus* Linstow; *D. facetus* Gussew; E—*D. parabramis* Gussew; F—*D. zandti* Bychowsky; G—*D. difformis* Bychowsky; H—*D. minor*; I—*D. linstowi* Bychowsky; J—*D. affinis* Bychowsky.

is incepted last of any part of the armature and approximately in its final location. In the beginning it has the shape of a straight or slightly bent, transversely elongated thread, just as occurs in the early stages of the development of the connecting plate of *D. longicopula* Bychowsky.

In a number of species, further development takes place only by means of the increase in dimensions of the supplementary plate without any change in its shape, in other plates it takes place with a change in shape and with unequal growth of separate sections of the plate. In order to avoid numerous repetitions, let us analyze the development of the complexly arranged supplementary plate in *D. cornu* Linstow (Fig. 146). After the formation of the plate in the shape of the curved thread, it begins to thicken and lengthen unequally in such a way that its middle part thickens much p. 146 more than the lateral ones. As a consequence, the supplementary plate acquires the shape of an isosceles triangle with a slightly invaginated lower edge. Further, the growth develops mainly in three directions, along the angles of the triangle, as a result of which is formed an inverted T-shaped plate with slightly sharpened lateral edges and with a more blunt upper edge which grows more intensively and soon the entire upper offshoot appears with edges which are parallel or even slightly widened toward the top lateral edges and a straight-cut upper edge. Approximately during this time the lateral edges reach their final lengths and the middle of the lower one, which was initially invaginated, begins to grow intensively forming a small, more or less rounded space in the center and somewhat straightening the line of the lateral growth and then forming two protuberances facing downward. Continuing to grow, the top offshoot widens more and more at its free end, which is divided, forming two slightly concave lobes which are characteristic of the final form of the plate. Somewhat back of the upper offshoot grow protuberances of the lower edge forming two growths which are slightly narrowed to the free end and lie parallel and close to each other. In such a fashion one can notice six stages of development: the first, a transversely elongated straight plate, the second, a curved stick-shaped plate, the third a triangle shape, the fourth an inverted T-shaped plate with a widening of the upper stem, the fifth the appearance of stems on the lower edge and finally the form corresponding to the connecting plate of the adult *D. cornu* Linstow. The division into these stages is, of course, arbitrary, their number can be decreased or perhaps more easily increased. It is important, however, that the structure of similar ones among the adult individuals of a great number of species of *Dactylogyrus* corresponds to the enumerated stages of development of the supplementary plate of *D. cornu.* As an example we will cite two species of *Dactylogyrus*

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[1] Perhaps the supplementary plates of certain species constitute an exception, specifically--*D. bicornis* Malewizkaja and *D. facetus* Gussew, among which they have a completely different structure.

which have supplementary plates corresponding to the separate stages of development in *D. cornu* (Fig. 146):

The first stage of the development of *D. cornu* supplementary plate corresponds to the plate in	(*D. cryptomeres* Bychowsky (*D. pulcher* Bychowsky
2nd to plate in	(*D. varicorhini* Bychowsky (*D. modestus* Bychowsky
3rd to plate in	(*D. macrocanthus* Wegener (*D. tuba* Linstow
4th to plate in	(*D. wunderi* Bychowsky (*D. nanus* Bychowsky
5th to plate in	(*D. zandti* Bychowsky (*D. linstowi* Bychowsky
6th to plate in	(*D. affinis* Bychowsky (*D. kulwieci* Bychowsky

The plan of development of the connecting plate in *D. cornu* obviously does not appear all-embracing. The plates of certain species cannot be included in it; however, using it as a base we can easily understand the process of development of a supplementary plate which has a different shape as for instance among *D. crucifer* Wegener and *D. frisii* Bychowsky and *D. minor* Wegener and *D. chalcalburni* Bychowsky. As was already indicated, *D. simplicimalleata* Bychowsky, *D. bicornis* p. 147
Malewizkaja and *D. facetus* Gussew, with an aberrant form of supplementary plates the development of which is not clear to us,are exceptions.

Thus, we have completed the description of the separate parts of the attaching apparatus of *Dactylogyrus*; certain interrelations in their development still remain to be shown. The middle hooks and the connecting and supplementary plates develop in relation to each other. One must consider it normal for the majority of the species that in the presence of stronger development of the middle hooks and their extensions, the connecting plate is more developed and the supplementary plate, where it exists at all, is more complex. This normality is a morphological expression of the functional increase in the role of the attaching armature during the attachment of the animal to its host and the mechanical fastening and the establishment of a determined size of the attaching disc. Because of this, the structure of the attaching armature of different species must be evaluated precisely from this point of view and then the different directions and ways of morphological changes become understandable. The same functional problems can be solved differently morphologically and at the expense of different parts of the attaching armature. For illustration of this condition we shall cite several examples. Among *D. anchoratus* (Dujardin) and the species close to it which do not have the supplementary plate, the interior extensions of the middle hooks are extremely elongated and it is they that support the upper edge of the attaching disc, strengthening and conditioning its fixed dimensions. The same problems among worms from the groups of *D. sphyrna* Linstow are solved constructionally differently, not by way of length but by a considerable widening of the interior stem of the middle hooks and, in addition to that, by the powerful development of one of the two pairs of the edge hooks which are increased twice in length and many times in width. Finally in the group of *D. kulwieci* Bychowsky the same role is fulfilled not by the offshoots of the middle hooks but basically by the supplementary plate which is strongly developed and almost reaches the dimensions of the middle hooks in length.

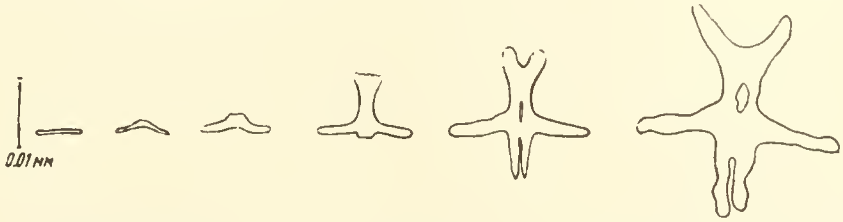

Fig. 146. *Dactylogyrus cornu* Linstow, the development of the supplementary plate of the attaching disc of worms from the gills of *Abramis brama* (L.) from the Bay of Finland near Peterhof. Explanation in text.

Concluding the description of the development of *Dactylogyrus* one must say a few words about the chitinous parts of the copulatory apparatus. Their inception takes place at rather early stages of the development and further growth and differentiation takes place rather quickly (just as that of the entire sex system). In connection with this, the worms become mature and first deposit eggs sometimes even before the final formation of the attaching armature. The last circumstance has a meaning in the work on systematics of a given genus and sometimes leads to undesirable results
when the stages of development of earlier known species are described as p. 148
individual species as happened in the works of Nybelin (Nybelin, 1936) and Alarotu (Alarotu, 1944). The duration of the development of *Dactylogyrus* from the free-swimming larva until adult mature individuals is very different. The most precise data were obtained by N. A. Izumova from *D. vastator* Nybelin (which are presented in the third chapter, page 104).

3. Development of *Dogielius* Bychowsky

The genus *Dogielius* appears to be the closest to *Dactylogyrus* and differs from the latter mainly in the structure and location of the middle hooks of the attaching apparatus (Fig. 147). They lie in one plane surface, are oriented with their points toward each other, and at the place of the transition of the point into the base part of the hook there is a characteristic "displacement" toward the interior so that the point is sharply delineated from the base part. In 1936 while describing the genus *Dogielius* (*D. forceps* Bychowsky) for the first time, we said on the subject: "We know that the difference in the shape of the middle hooks serves as a good systematic character of a species, but in addition to that, the difference has a completely different qualitative meaning in this case. Actually, as a rule the differences lead to a larger or smaller development of certain parts, principally of the same hook.... Here also we have a difference connected with a change of the shape of the hook which stands independently of larger or smaller developments of the separate parts and apparently which appears during the early stages of ontogenesis..., and consequently, its middle hooks (*Dogielius forceps* Bychowsky) already differ from those in *Dactylogyrus* in the early stages of development." These suppositions were fully substantiated later during the research in 1944 on a second type of *Dogielius*. This type (*D. planus* Bychowsky) was discovered by us on *Schizothorax intermedius* MacClelland in the river Varzob near Stalinbad; its development was studied rather completely by us with the exception of the earliest stages, as we were unable to obtain egg-laying.

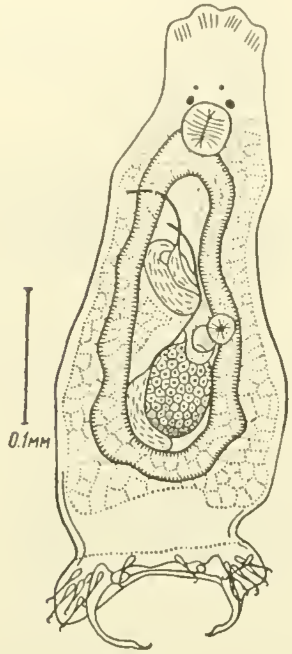

Fig. 147. *Dogielius forceps* Bychowsky, general view of the worm from the gills of *Schizothorax pseudakaaiensis issykkuli* Berg from the Tsku (Kazak Republic of SSSR).

The youngest (known, *nobis*) larvae of *Dogielius* (Fig. 148, A) have the head end still with two lobes. The edge hooks numbering 14 are 0.016 - 0.017 mm in length with a well-developed terminal little hook and basal part of the handle. The later terminates in a sphere-shaped widening corresponding to the proximal part of the handle.[1] Further growth of the

TABLE 3

Correlation of the size of separate parts during the development of *Dogielius planus* Bychowsky (in mm)

Length of body	Length of edge hooks	Length of sharp edge	Length of basal part plus extension	Width of upper edge	Length of connecting plate	Copulatory organ	Note
0.08	0.016-0.017	0.012	0.007	0.001	0.016	None	
0.09	0.017-0.018	0.012	0.024	0.001	0.026	None	Middle hooks on the terminal place
0.12	0.018-0.019	0.012	0.030	0.002	0.027	None	
0.09	0.018-0.019	0.012	0.045	0.003	0.030	None	Beginning of the formation of the extension
0.12	0.019-0.020	0.012	0.054	0.006	0.035	First traces of inception	
0.10	0.018-0.020	0.012	0.055	0.013	0.039	Tube formed	
0.16	0.020-0.021	0.012	0.062	0.014	0.044	Extension forms lateral outgrowth	
0.20	0.020-0.021	0.012	0.065	0.016	0.045	Almost developed	
0.25	0.020-0.023	0.012	0.070	0.020	0.046	Fully developed	Mature worm

p. 149

lateral hooks takes place rather slowly so that the middle hooks succeed
in growing almost up to their final dimensions during the same period,
(Table 3). The location of the edge hooks of the youngest larva is charac- p. 149
teristic: the hooks are located along the edge of the disc (with the exception
of the 7th pair lying almost in the center of the disc), and the hooks of the
6th pair are separated from each other somewhat further than from the
others and are oriented with their terminal hooks toward each other
locating themselves in such a way and in the same place as the middle
hooks will be located subsequently. The latter are already present but are
located above the center of the disc (with the upper edge even extending
beyond it, Fig. 148, A). As we had supposed in 1936, they already have a
characteristic shape with the "displacement" between the basal part and the
point. The point is already of final length but is still thin and frail, just
as the base part, represented by a straight little stick two times smaller
than the hook part, which is also frail and thin. The connecting plate also
exists in the shape of a straight or slightly curved thread only a little
shorter than the middle hooks. It lies freely between the middle hooks.
Very soon after the stage described, the middle hooks descend to the lower
edge of the disc, displace the 6th pair of edge little hooks laterally and cut
through, thus assuming their final position. At this time, their base part
is already one and one-half to two times longer than the tip of the hook
(Fig. 148, C). Further development of the middle hooks of *Dogielius*
(Fig. 149, A) takes place just as among *Dactylogyrus* by way of the thicken-
ing of the parts which were incepted earlier and the accretion of the basal
part at its free end and then the widening of the free ends and the formation
of the interior and exterior extensions which almost merge and form, so
to speak, a widened triangular plate. The growth of the connecting plate p. 150
(Fig. 149, B) parallels the growth of the middle hooks, reaches its final
length rather slowly and begins to thicken in proportion with its final shape.
The development of internal organs takes place in the same way as among
Dactylogyrus. The copulatory organ (Fig. 150) is incepted at the time when
formation of the widening corresponding to the extensions of the middle
hooks has already begun. At first it has the shape of a thin, almost straight p. 151
pipe with a weakly developed base from which departs the supporting appa-
ratus in the shape of a band with a small widening in its upper third and
with a sharpened free end. Further growth takes place rather quickly by way
the shape of an increase in the volume and size of the pipe and of the base
and of the growth and complexity of the terminal and of the supporting
apparatus. The copulatory organ acquires its final form at the same time
as the termination of the growth of the parts of the attaching armature.

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[1] Judging by the head end, by the structure of the edge hooks, and by the location of the middle hooks of the larva, the latter became attached to the host and lost its ciliary epithelium very recently.

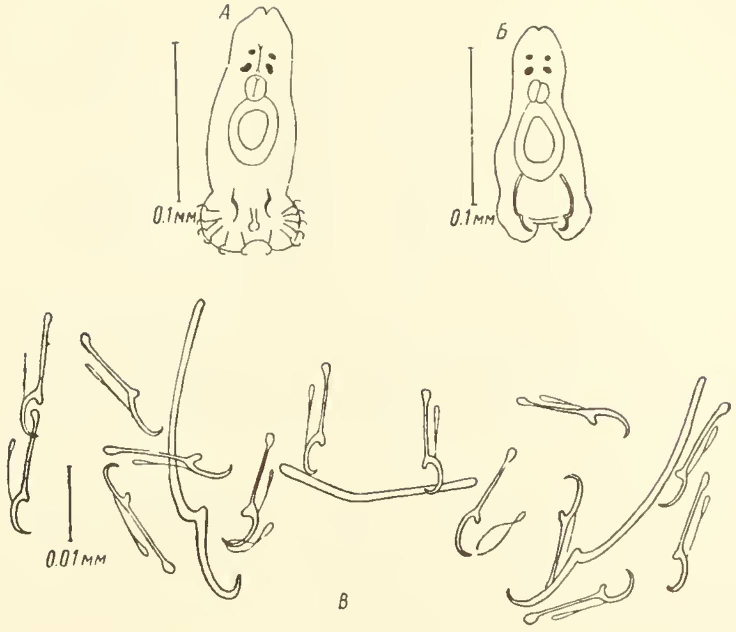

Fig. 148. Dogielius planus Bychowsky, larvae from the gills of Schizothorax intermedius McCl. from the river Varzob (Tadjikistan, SSSR). A--General view of a larva which has just settled on the gills; B--General view of a more fully grown larva; C--Attaching armature of a more mature larva.

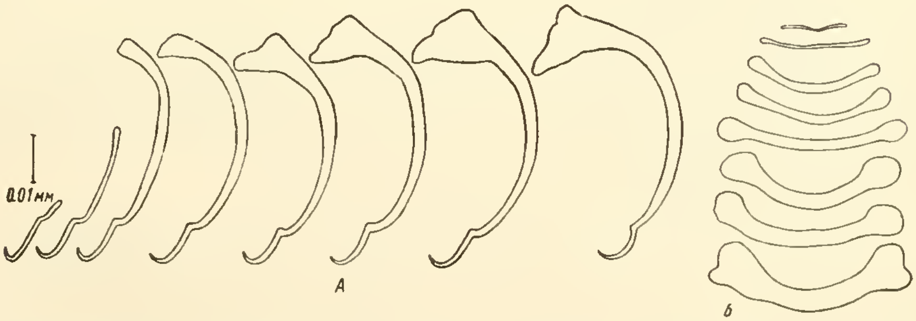

Fig. 149. Dogielius planus Bychowsky, stages of development of the attaching apparatus from the gills of Schizothorax intermedius McCl. from the river Varzob (Tadjikistan, SSR). A--Stages of development of middle hooks; B--Stages of Development of the connecting plate of the middle hooks.

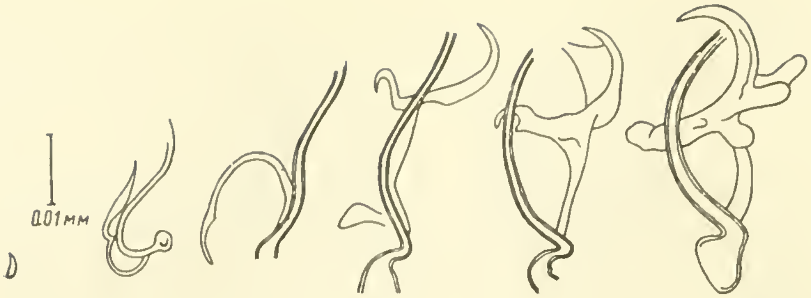

Fig. 150. *Dogielius planus* Bychowsky, stages of development of the copulatory organ of the worms from the gills of *Schizothorax intermedius* McCl. from the River Varzob (Tadjikistan, SSSR).

4. The development of *Ancyrocephalus* Creplin

We accept the genus *Ancyrocephalus* in the broad sense in the present work. The reason for this appears to be the extremely formal approach of American researchers toward the description of new genera of Ancyrocephalinae and the lack of the opportunity to conduct a special revision of this interesting group at the present time. Undoubtedly, however, considered in such scope this genus is artificial and demands subdivision. It seems to us that from *Ancyrocephalus* (*s. lat.*) one can isolate several independent groups (apparently the actual genera), on one hand, the group of forms with the type of the genus, *Anc. paradoxus* Creplin, which have intestinal trunks not merging with each other, and on the other hand, the second group of species with merging intestinal trunks to which are related first of all well-known types; *Anc. cruciatus* (Wedl.), *Anc. vanbenedeni* Parona and Perugia (for more details see the chapter, "A System of Monogenetic Trematodes" pages 348-352).

The genus *Ancyrocephalus* (*s. lat.*) basically resembles *Dactylogyrus* Diesing in its structure but differs by the presence of four middle hooks on the attaching disc, each pair of which is connected by a special plate. The disc doesn't bear any supplementary chitinous formations. Both connecting plates are more or less of a simple form and never articulate with each other. The edge hooks are ordinary and number 14.

In connection with the above-mentioned understanding of the genus the description of the development is given according to representative species, because generalized data can subsequently lead to faulty representations concerning the systematics of the group. Certain considerations of general order are expressed at the end of the section.

Ancyrocephalus paradoxus Creplin--During our work at Saratov in July 1947 we succeeded in hatching a free-swimming larva of Anc. paradoxus Creplin from the eggs of the parasite from the gills of Sandre [Lucioperca lucioperca (L.)]. The development of the larva in the egg p, 152 took place in four days at temperatures of 20 to 24°. The larva which had emerged from the egg had a length of about 0.15 mm with a width of about 0.05 mm (the egg having the length of about 0.10 and the width of about 0.06 mm). The mature adult worm has an average length of about 2 mm, i.e., 13-14 times longer than the larva. The latter have a ciliary epithelium located in essentially the same fashion as among the larvae of Dactylogyrus, i.e., in three zones or belts. The attaching disc of the larva is not at all delineated from the body and is equipped with 14 edge hooks beside which there are no traces of chitinous formations so that the inception of the middle hooks takes place later. The edge hooks have the length of about 0.015- 0.018 mm; their hooked part is well-developed but the handle is weak with a small widening at its free end (Fig. 151). Among adult worms (Fig. 152) the edge hooks have the length of about 0.016 to 0.019 mm, i.e., they are almost completely of the same sizes as in the larva. Judging from the observations on live mature worms, their edge hooks hardly function whereas among the young forms, which have fully formed middle hooks, the edge hooks still function fairly actively. The larvae have two pairs of relatively large eyes. The internal structure of the larva is completely analogous to that of the larva of Dactylogyrus. Further development has not been followed through. The youngest known individuals from the hosts which were at our disposal are about 0.5 mm in length and already have fully formed attaching and sex armatures.

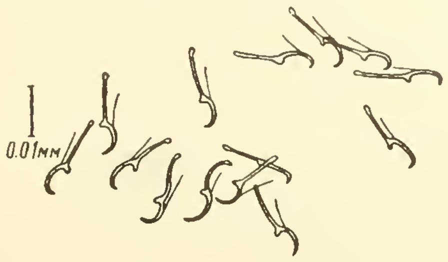

Fig. 151. Ancyrocephalus paradoxus Creplin, attaching armature of the free-swimming larva.

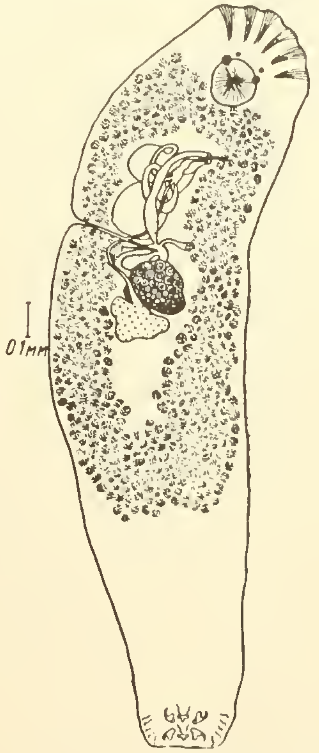

Fig. 152. Ancyrocephalus paradoxus Creplin, adult worm from the gills of Lucioperca lucioperca from Ahchtarin estuaries (Sea of Azov).

Ancyrocephalus (*s. lat.*) *cruciatus* (Wedl.)--We also know only the structure of the free-swimming larva of *Anc. cruciatus* (Wedl.). It was obtained by us seven days after the deposition of the eggs by the worm, from the gills of the Viun [*Misgurnis fossilis* (L.)], in June 1938 (at the Peterhof Institute of Natural Science near Leningrad). The larva is 0.12 mm in length and has a width of 0.03 mm. The head end has weakly expressed lobes. p. 153 Two pairs of eyes are strongly developed. The ciliary epithelium is located in the same fashion as it is in *A. paradoxus* Creplin. The attaching disc is weakly expressed. On it are located 14 edge hooks (Fig. 153) of the usual dactylogyrid form, about 0.017 - 0.018 mm in length and with the length of the terminal hook about 0.006 mm. These dimensions remain without change also among adult worms. The first pair of middle hooks in the shape of plates of about 0.020 mm in length which are slightly curved and sharpened on the lower end, already lies in the center of the attaching disc along with the edge hooks. Besides that, a slightly curved very tender connecting plate of the first pair of middle hooks lies freely between them. It is about 0.008 mm in length. There are no traces of the second pair of middle hooks or of their connecting plate. In such a fashion we see a different development in time of the middle hooks in *Anc. cruciatus* (Wedl.), and the inception of the first pair takes place even during the embryonic development considerably earlier than the appearance of the traces of the second pair. As is known, the adult *Anc. cruciatus* (Wedl.) (Fig. 154) has a structure of the middle hooks and of the connecting plates similar to that of *Dactylogyrus* and also a similar inner organization, so that one can easily visualize, in general character the progress of further development with the exception of the correspondence of stages of development of separate parts in time. In connection with the latter, one can indicate that the growth of the first pair of middle hooks continues after the inception of the second pair, for we observed young immature worms with underdeveloped hooks on both pairs.

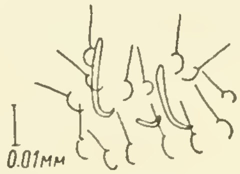

Fig. 153. *Ancyrocephalus* (*s. lat.*) *cruciatus* Wedl, attaching armature of a free-swimming larva.

Ancyrocephalus (*s. lat.*) *vanbenedeni* (Parona and Perugia)--During the work at Karadaga Biological Station in August of 1957 we hatched the larva of *A. vanbenedeni* several times. The period of development in all instances was about 4 days. The larvae which emerged from the eggs had a length of about 0.075 mm with a width of about 0.025 mm. The larva (Fig. 155) is torpedo-shaped with a powerfully developed "little tail" at the posterior end. The ciliary epithelium is distributed in three zones just as among the preceding species. The attaching disc has 14 edge hooks; no traces were discovered of the middle hooks in the process p. 154 of inception. The edge hooks are of identical shape with a weakly expressed handle; their length is very insignificant--about 0.01 mm. Among adult forms the sizes of the edge hooks are the same and consequently no growth is observed among the latter in the post-embryonic period. Further development has not been followed through. The middle hooks of adult worms are more or less of the same sizes (Fig. 156); apparently the ventral pair is incepted first. In spite of the fact that this species is encountered both in marine and fresh water the development of the eggs apparently takes place only in sea water, for our attempts to obtain larvae in fresh water were not successful.

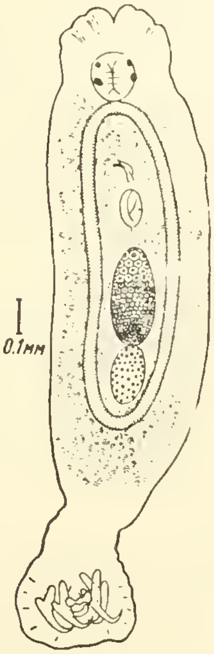

Fig. 154. *Ancyrocephalus* (*s. lat.*) *cruciatus* Wedl., adult worm from the gills of *Misgurnus fossilis* (L.) from the region of Peterhof (Leningrad region).

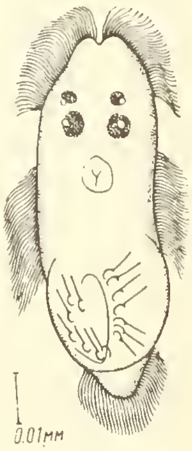

Fig. 155. *Ancyrocephalus* (*s. lat.*) *vanbenedeni* (Parona and Perugia), free-swimming larva.

Ancyrocephalus (*s. lat.*) *mogurndae* (Yamaguti). Certain data concerning the development of this species, discovered in Lake Hanka in 1948-1949 on the gills of *Sineperca chua-tsi* (Bas.) are reproduced in the works of A. V. Gussew (1955). He writes: "The development continued about 3 days (65 hours) at an air temperature on the first day of about 27° centigrade, the second--21° to 26°, and the third--18° to 22°. The larva has a length of about 0.06 and a width of about 0.02 mm, it has 4 little eyes with little lenses, is equipped with three zones of cilia, on the anterior end, along the sides of the equatorial region and on the posterior (the latter is somewhat displaced toward the dorsal side). The attaching disc is closed. Its armature (Fig. 157--B. B.) consists of 7 pairs of edge hooks with lengths of about 0.015 - 0.017 mm. There are no traces of the middle hooks." In addition to that A. V. Gussew indicates that, "that on the gills of the perch-bass (*Sineperca*--B. B.) one immature individual with a length of 0.34 mm and a width of 0.09 mm and with fully developed middle hooks which have the same common length--0,048 mm and the point 0.019 mm--was found. The ventral connecting plate is still tender, 0.005 x 0.042 mm. The dorsal connecting plate is very thin and apparently is incepted after the ventral one during the development (just as the dorsal hooks), its sizes are 0.002 x 0.055 mm. The copulatory organ and the vaginal armature begin to form in the shape of thread-like pipes and three plates corresponding to the terminal part of the supporting apparatus." The adult worms (Fig. 158) have edge hooks 0.015 - 0.019 mm in length and thus one can consider that no growth is observed among edge hooks of this species, just as among the preceding ones.

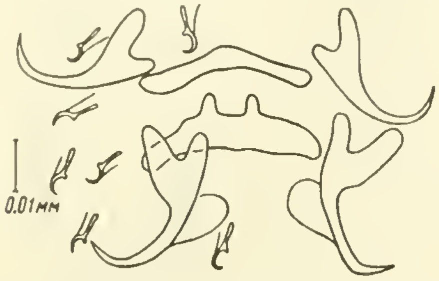

Fig. 156. Ancyrocephalus (s. lat.) vanbenedeni (Parona and Perugia), attaching armature of the disc of an adult worm from the gills of Mugil auratus Risso from the region of Karadaga (Black Sea).

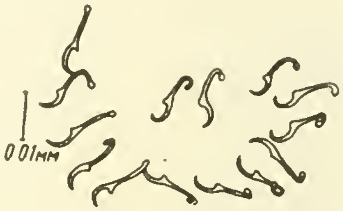

Fig. 157. Ancyrocephalus (s. lat.) mogurndae (Yamaguti), attaching armature of a free-swimming larva. (According to Gussew, 1955).

Ancyrocephalus (s. lat.) curtus Akmerow.--This worm de-
scribed from the Reservoir of Amur from Percottus glehni (Dyb.) was
studied by A. V. Gussew in 1948 - 1949 in Lake Hanka. He hatched many p. 155
larvae and the period of development of their eggs was about 5 days. The
length of the larva was about 0.09 mm and the width 0.03 mm. Their
structure is typical: they have three zones of ciliary covering; their
intestine is circular with a large pharynx. The armature of the attaching
disc (Fig. 159) consists of 14 edge hooks--0.015 to 0.017 mm in length
and a pair of chitinous thin brackets (embryonic inceptions of the ventral
pair of middle hooks) about 0.016 mm in length. In addition to this,
A. V. Gussew once found an immature young worm which still possessed
undeveloped dorsal middle hooks and their connecting plate, while having
fully formed ventral hooks and their plate. Adult worms (Fig. 160) have
edge hooks 0.016 - 0.020 mm in length, that is they grow somewhat in the
postembryonic period. This growth proceeds by way of an increase of
the round terminal part of the handle which is developed more weakly among
young worms.

Ancyrocephalus (s. lat.) pavlovskyi Gussew--In 1948-1949 A.
V. Gussew obtained larvae of this species on Lake Hanka. The develop-
ment of the eggs continued about 4 days. The larva has three zones of
cilia the first--of eight cells, an equatorial--along the sides of the body p. 156
of 4 (6?) ciliary cells, and a posterior one (the quantity of the cells has
not been determined). The attaching disc (Fig. 161) with 7 pairs of edge
hooks 0.013 - 0.016 mm in length and a pair of powerful sabre-
shaped inceptions of the ventral middle hooks of about 0,02 mm in length.

Ancyrocephalus (s. lat.) hemibarbi Achmerow--The larvae of this species were obtained by A. V. Gussew of Lake Hanka in 1948-1949. The embryonic development (in hanging drops) required 4 to 5 days. The larva has three zones of cilia. The attaching disc is equipped with 7 pairs of p. 157

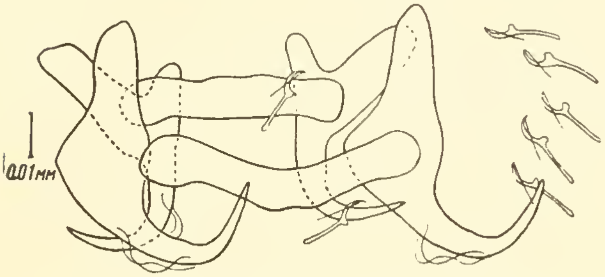

Fig. 158. Ancyrocephalus (s. lat.) mogurndae (Yamaguti), attaching armature of the disc of an adult worm from the gills of Siniperca chua-tsi (Bas.) from the Island of Hanka.

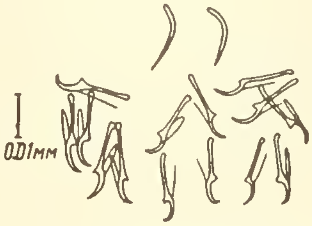

Fig. 159. Ancyrocephalus (s. lat.) curtus Achmerow, attaching armature of a free-swimming larva. (According to Gussew, 1955).

edge hooks, 0.012 to 0.014 mm in length and one pair of powerful sabre-shaped inceptions of the ventral middle hooks (Fig. 163); the length of the latter is about 0.025 mm. The adult worms, which parasitize the same fishes as the preceding type, have the usual attaching armature (Fig. 164).

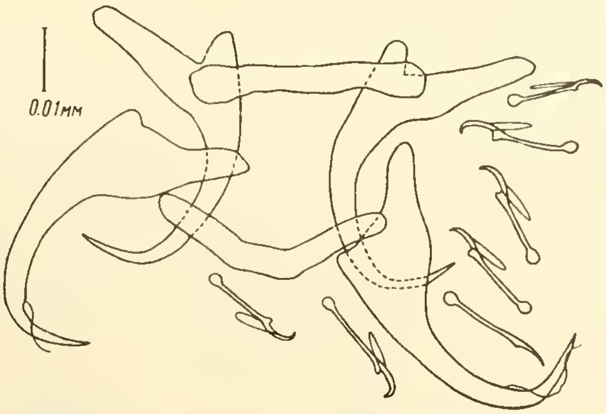

Fig. 160. Ancyrocephalus (s. lat.) pavlovskyi Gussew, attaching armature of the disc of an adult worm. (According to Gussew, 1953).

The edge hooks are also of two types; however, the difference between them is considerably less than among A. pavlovskyi Gussew. Thus there are only two small hooks, the 6th pair. Their length is 0.016 to 0.018 mm. All the remaining hooks have a length of 0.025 to 0.039 mm (the smallest among them is the 7th pair).

Thus, from the existing incomplete material on the development, more precisely according to the larvae, it is apparent that in Ancyrocephalus the situation is much more complex than among the preceding types. Thus, from the seven species which have been examined, on three the middle hooks are incepted in the postembryonic period, whereas among five (sic) species the inceptions of the first pair of middle hooks are already formed at that time. In one species the connecting plate of the ventral (first. pair) of the middle hooks is also incepted in the embryonic period. The fate of the edge hooks also varies. Among 4 species they remain without change during the entire life of the worms, whereas, among three species they grow more or less intensively during the postembryonic period. It is impossible not to note that among forms which have hooks which do not grow, in a majority (among 3 out of 4), the middle hooks are incepted

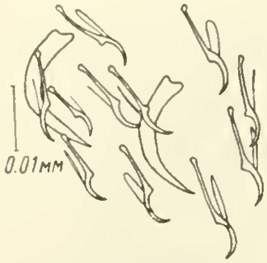

Fig. 161. Ancyrocephalus (s. lat.) pavlovskyi Gussew, attaching armature of the free-swimming larva. (According to Gussew, 1955).

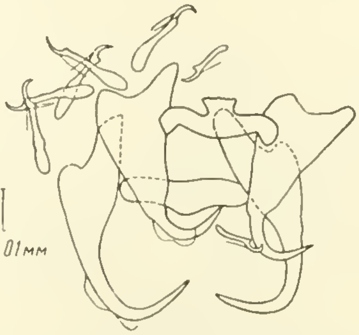

Fig. 162. Ancyrocephalus (s. lat.) pavlovskyi Gussew, attaching armature of the disc of an adult worm from the gills of Hemibarbus maculatus Bl. (According to Gussew, 1955).

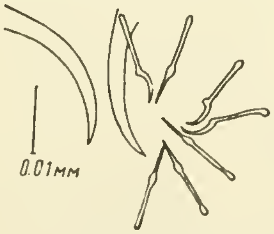

Fig. 163. Ancyrocephalus (s. lat.) hemibarbi Achmerow, attaching armature of a free-swimming larva. (According to Gussew, 1955).

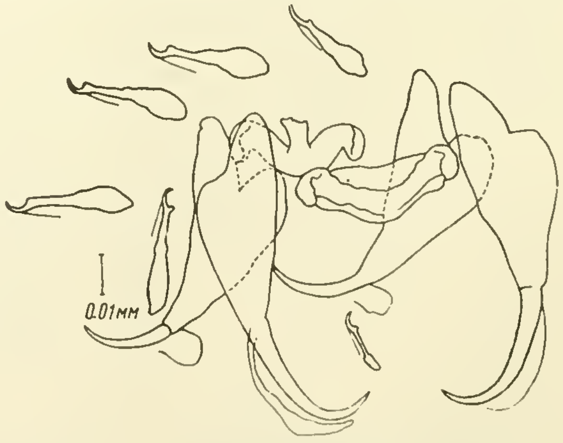

Fig. 164. Ancyrocephalus (s. lat.) hemibarbi Achmerow attaching armature of the disc of an adult worm from the gills of Hemibarbis maculatus Bl. (According to Gussew, 1955).

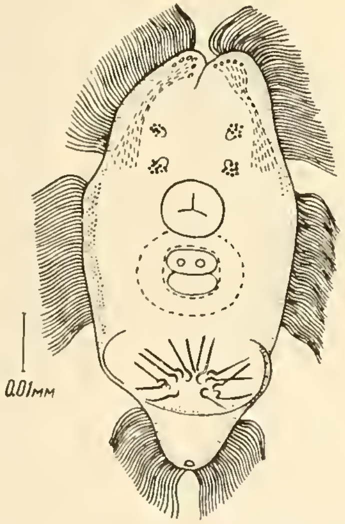

Fig. 165. Protancyrocephalus strelkowi Bychowsky, free-swimming larva.

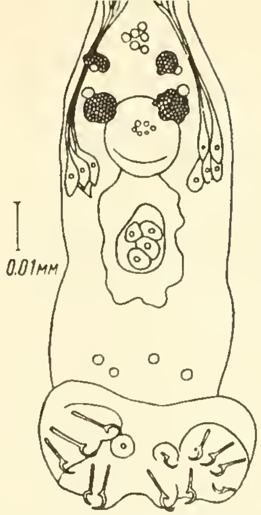

Fig. 166. Protancyrocephalus strelkowi Bychowsky, the larva which has just settled on the gills of Limanda aspera (Pallas), from the region of Yablochnoii (Southern Sakhalin, Sea of Japan).

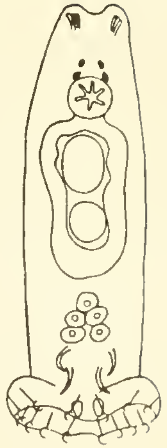

Fig. 167. Protancyrocephalus strelkowi Bychowsky the stages of development showing the middle hooks which are beginning to develop. Gills of Limanda aspera (Pallas) from the region of Yablochnoii (Southern Sakhalin, Sea of Japan). Freehand drawing, semischematically.

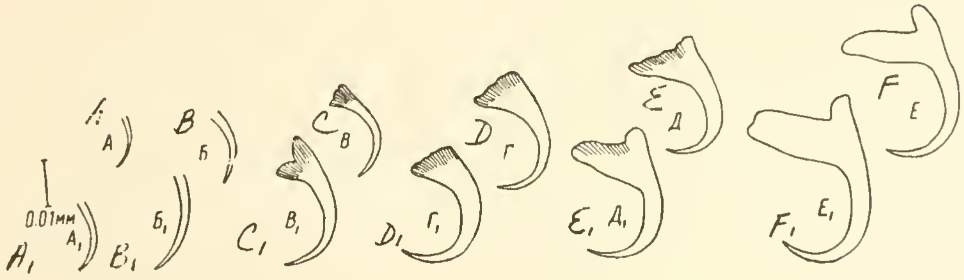

Fig. 168. Protancyrocephalus strelkowi Bychowsky, stages of development of the middle hooks. Explanation in text.

p. 158

during the postembryonic period. This can scarcely be a pure coincidence. In conclusion one must say that the system of the Ancyrocephalinae as a whole demands a rather substantial and careful revision, and that the first priority should be given to the study of the species, which are so far classified by us in the genus *Ancyrocephalus*.

5. The development of *Protancyrocephalus* Bychowsky

During our work on South Sakhalin in 1946 and on the Island of Shikotan in 1949, we studied the development of a new species and genus of Ancyrocephalinae—*Protancyrocephalus* *strelkowi* Bychowsky parasitizing the gills of young flounders, Lemanda aspera (Pallas). The absence of connecting plates between the two pairs of middle hooks appears to be a characteristic trait (of this species, *nobis*). The basic traits of organization are clear from the drawing of the adult form.

The development of *Pr.* *strelkowi* from the moment of egg-deposition to the emergence of the free-swimming larva takes place during 8 to 11 days at average temperatures of 18° to 20°. The free-swimming larva of this type has a length of 0.08 - 0.10 mm, it has a relatively blunt anterior end and an elongated and sharpened posterior end (Fig. 165). The ciliary covering is distributed just as it is among the larvae of *Dactylogyrus*, but both anterior groups do not merge at their anterior ends, whereas the third group consists of two clearly divided sections of ciliary epithelium lying along the sides of a special cone which is more sharply expressed than in *Dactylogyrus* and falls off at the same time as the ciliary epithelium. The attaching disc is already delineated from the body at the time of emergence of the larva from the egg, but the 14 edge hooks have not yet cut through at this time and lie with their points oriented toward the center of the disc. Their length is about 0.015 mm with terminal little hooks about 0.005 mm. There are two groups of head glands and four well-developed pigmented eyes in the free-swimming larva just as in the adult animal. The digestive system is of the customary type with a large pharynx and circular intestine. The nervous system is almost invisible with the exception of the more noticeable head ganglia located at the level of the eyes. The excretory system is unnoticeable. The development of edge hooks takes place as usual, p. 159
their growth is insignificant because among fully matured egg-laying individuals the edge hooks have a length of not more than 0.018 - 0.020 mm. The larvae which have just settled on the gills[1] have 4 large transparent

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[1] We observed the settling of the larva on the gills during the entire time of study (July-September): however, in the Bay of Anam on the Island of Shikotan this process was of more concentrated nature (occurring, *nobis*) at the end of July--beginning of August. In our diary it is noted that the

cells in the interior of the body somewhat above the attaching disc which apparently play a role in the formation of the middle hooks. The latter are incepted in their places almost simultaneously and descend to the disc together (Fig. 167). However, certain differences are observed in the tempo of their growth: the first pair grows somewhat faster and among the mature animals it was slightly but distinctly larger than the second pair. The nature and the sequence of the development of middle hooks are the same as among *Dactylogyrus* (Fig. 168). The copulatory organ is incepted in the shape of a pipe of almost the same shape and size as among adult animals but with a weakly developed base which grows rather slowly (Fig. 169). The time of inception of the copulatory organ coincides with the beginning of the formation of the extensions of the second pair of middle hooks.

6. The development of *Ancylodiscoides* Yamaguti

The genus *Ancylodiscoides* (Fig. 65), established in 1937 by Yamaguti, pertains to Ancyrocephalinae and is characterized mainly by the structure of the attaching apparatus, which consists of 14 very small edge hooks and 2 pairs of middle hooks. The latter are of different sizes and the interior offshoots of the large pair are equipped with supplementary plates articulating with them (Fig. 170). There are four eyes. The intestinal trunks merge at the posterior end. The sex system (is equipped, *nobis*) with a strongly developed chitinous copulatory organ and vaginal pipe (the latter is sometimes absent). They parasitize Siluridae and Bagridae. At the present time there is a number of materials (papers, *nobis*) about the development of the representatives of this genus. Thus Siwak (Siwak, 1932) in a work dedicated to the description of *A. vistulensis* Siwak from the gills of the European *Silurus* reproduces a drawing of a free-swimming larva of this type and presents his observations on the development and further growth of the larvae. A. V. Gussew in 1948-1949 hatched the free-swimming larvae of *A. strelkowi* Ackmerow and *A. varicus* Ackmerow. Finally, during our work in the Delta of the Volga in July, 1932 we sketched one of the later stages of development of *A. siluri*

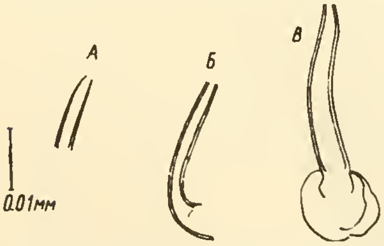

Fig. 169. *Protancyrocephalus strelkowi* Bychowsky, stages of development of the copulatory organ. Explanation in text.

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entire mass of larvae which were found at this time on the fishes were in absolutely the same stage of development. Thus, the deposition of eggs among these forms takes place extremely rapidly (see chapter on life cycles, page 111).

Zandt and in August, 1953, we also hatched larvae of this type, and presumably *A. vistulensis* Siwak and observed a number of subsequent stages of their development.

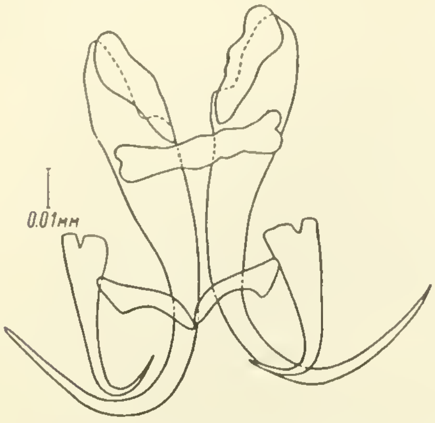

Fig. 170. *Ancylodiscoides siluri* (Zandt), middle hooks of the disc of the adult worm from the gills of *Silurus glanis* L. from the Delta of the Volga.

The development of the eggs of *Ancylodiscoides* takes place in from 3 to 6 days depending upon temperature. The larva which has just emerged from the egg (Fig. 171) is of the same shape and structure in all species as the larvae of p. 160 *Dactylogyrus*, but differs in the fact that its attaching armature (Fig. 172) has two middle hooks in addition to the edge hooks (14 and not 12 as Siwak erroneously indicates). The latter are incepted above the edge hooks in the shape of chitinous little parentheses just as takes place among *Anchyrocephalus* (*s. lat.*) *cruciatus* Wedl. but in opposition to the latter, the connecting plate of this pair is as yet absent, it is incepted later.

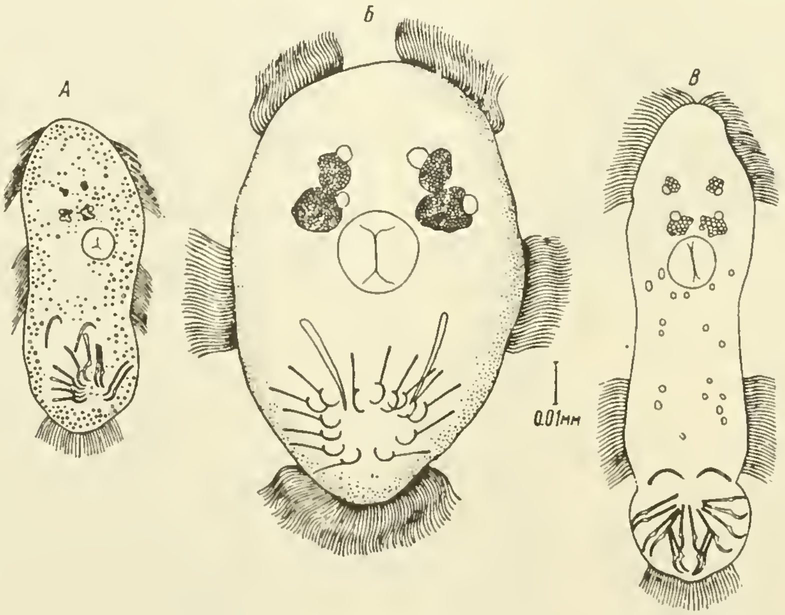

Fig. 171. *Ancylodiscoides* sp. sp. free-swimming larvae, A--*A. vistulensis* (Siwak), the larva is enlarged 400 times (According to Siwak, 1932); B--*A. siluri* (Zandt); C--*A. strelkowi* Ackmerow.

The sizes of the larvae: *A. vistulensis*--according to our preparations the length is 0.06 - 0.08 mm and the width is 0.02 - 0.04 mm and correspondingly 0.11 and 0.04 mm, according to the data of Siwak; the length of the edge hooks is 0.015 - 0.016 mm and the inceptions of the middle hooks 0.016 - 0.019 mm; in *A. siluri* the length is 0.05 - 0.08 mm and the width is 0.02 - 0.04 mm and the length of the edge hooks is the same as in the preceding species and the length of the middle hooks is 0.022 - 0.026 mm; *A. strelkowi*--length up to 0.15 mm, the width being 0.03 mm, the length of the edge hooks 0.013 - 0.015 mm and the inceptions of the middle hooks 0.012 mm; *A. varicus*--the length and the width of the larva has not been established by A. V. Gussew, the length of the edge hooks is 0.013 - 0.015 mm and of the inceptions of the middle ones 0.015 mm.

p. 161

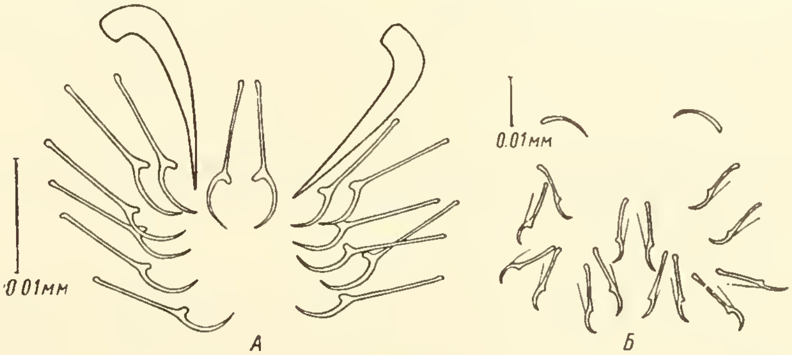

Fig. 172. *Ancylodiscoides* sp. sp. attaching armature of the free-swimming larvae. A--*A. siluri* (Zandt); B--*A. strelkowi* Achmerow.

The edge hooks among representatives of this genus apparently either do not grow completely or almost completely and retain their embryonic traits. Siwak indicates that during the further development of the larva of *A. vistulensis* the first pair of middle hooks reaches considerable length and is already equipped with a connecting plate when the second pair is incepted. At that time the larva reaches 0.15 mm in length, the first pair reaches final sizes when the larva is 0.23 mm long whereas the second pair develops in full toward the time of the cessation of the growth of the worm (length 0.74 - 1.14 mm). According to our observations on *A. vistulensis*, which in general are similar to the data of Siwak, the first pair of middle hooks and their connecting plate reach the final stage of their development before the inception of the second pair (Fig. 173, A). The latter is incepted in the shape of two slightly curved little parentheses above the attaching disc (Fig. 173, B) and reaches rather large sizes before the second connecting plate begins to p. 162 form. The supplementary plates are incepted last. The chitinous armature of the sex system has already begun to form about that time.

The development of *A. siluri* takes place in a similar fashion to that of *A. vistulensis*. Apparently during the early stages the difference is expressed only in the sizes of the body and the chitinous parts of the attaching disc. However, during later stages among *A. siluri* one observes a certain delay in the inception of subsequent elements along with a larger size of hooks. Thus, middle hooks of the first pair reach

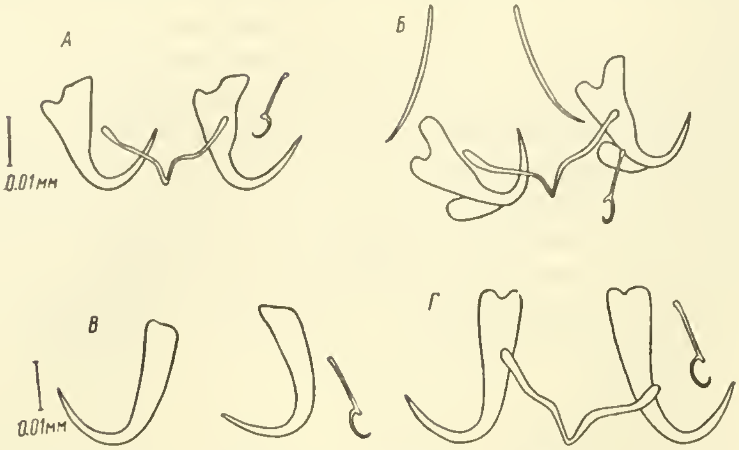

Fig. 173. Ancylodiscoides sp. sp., attaching armature of a developing larvae from the gills of Silurus glanis L. from the Delta of the Volga. Explanation in the text.

considerable size (Fig. 173, C), whereas the inceptions of their connecting plate is not yet observed. Later, even though the first pair of middle hooks and their plate are fully formed the inception of the second pair will still not be observed for a long time (Fig. 173, D).

After the inception of the second pair of middle hooks the larva grows rather slowly. During that time the larva (Fig. 174) has a length of about 0.23 mm and a width of 0.08 mm (in a somewhat compressed condition). The edge hooks are of final shapes and sizes (0.015 - 0.017 mm, i.e., they have grown scarcely noticeably)--the first pair of the middle hooks is of the customary shape for the adult worm; its sizes: length 0.024 mm, the basal part 0.022 mm, the interior offshoot 0.009 mm, the exterior 0.003 mm and the edge or point 0.015 mm. The connecting plate is fully developed, its length is 0.040 mm. Above the attaching disc lie two middle hooks in the shape of parallel parentheses which are curved at the upper end and

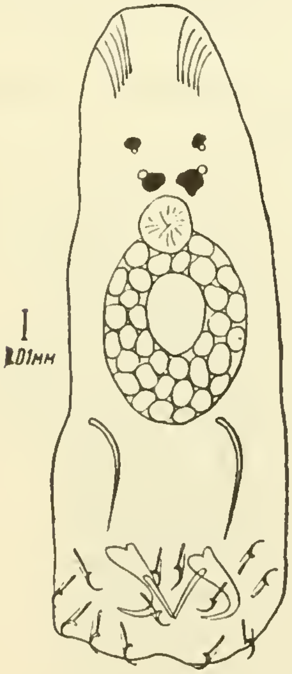

Fig. 174. Ancylodiscoides siluri Zandt, the larvae with the recently formed second pair of middle hooks on the attaching disc, from the gills of Siluris glanis L. from the Delta of the Volga.

sharpened in the lower part, and which have a length (along the curve) of about 0.040 mm. There are no traces of the connecting plate of the second pair. The eye spots are of the usual form and location. The digestive system has a rounded pharynx, 0.02 mm in diameter, and circular intestine without traces of the posterior blind growth characteristic of the *A. siluri.* There aren't any traces as yet of the sex armature.

Subsequent development has not been followed through, but its progress is evident.

All in all, one can note that the development of representatives of *Ancyclodiscoides* is close to that of *Ancyrocephalus* which has larvae with the inceptions of middle hooks and differs sharply from the development of *Protancyrocephalus* among which the process of formation of the middle hooks proceeds simultaneously.

7. The development of *Bychowskyella* Achmerow

The genus *Bychowskyella*, described in 1952 from Amur Bagridae by A. H. Achmerow, resembles *Ancylodiscoides* in its structure, but is easily distinguished by its peculiar armature of the attaching disc (Fig. 175). The latter carries two pairs of middle hooks of different size,

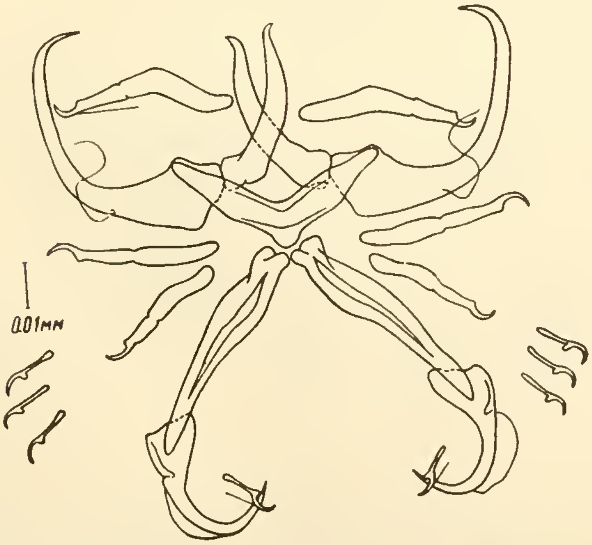

Fig. 175. *Bychowskyella pseudobagri* Achmerow, attaching armature of an adult worm from the gills of *Pseudobagrus fulvidraco* (Rich.) from the Island of Hanka.

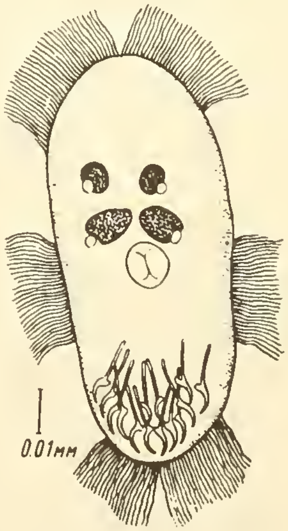

Fig. 176. *Bychowskyella pseudobagri* Achmerow, free-swimming larva.

one unpaired connecting plate (of the second pair of middle hooks), two connecting plates of the first pair of middle hooks and a pair of supplementary plates, articulating with the body of the second pair of middle p. 163 hooks; the edge hooks are of two types; 4 pairs of small ones which preserve embryonic shapes and sizes and three pairs of large ones with massive handles. A. V. Gussew in his work on Monogenoidea of the fishes of Lake Hanka (1955) describes a free-swimming larva in one of the latter stages of development of *B. pseudobagri* Achmerow. The development in the eggs takes place in four days at temperatures of 16 - 21°. The larva which has just emerged from the egg is torpedo-shaped with 3 zones of cilia located just as among *Dactylogyrus* (Fig. 176). Gussew succeeded in counting, approximately, the number of cells in each of the ciliary zones. Thus, the first zone consists of 9 + 9 (the very p. 164 anterior end of the body of the larva is free of ciliary cells), the middle of 6 + 6 (can be 7 + 7) and finally the posterior, unpaired and lying in the shape of a little cap on the dorsal side behind the disc--of 12(?) ciliary cells. The larva (is equipped, *nobis*) with 4 well-developed eyes. The attaching disc (Fig. 177) is equipped only with 7 pairs of edge hooks, 0.013 - 0.017 mm in length. There are no traces of other armature. In addition to that, Gussew writes in his work: "Besides the mature worms we found one young specimen of this type in which the ventral middle hooks (the first pair according to our terminology--B. B.) were almost formed (their length is 0.027 mm, the length of the point is 0.013 mm), their connecting plates are yet without articulated little heads (their length is 0.027, their thickness is 0.003 mm), the dorsal middle hooks (second pair--B. B.) are as yet without a body, and are represented only by the point and its narrowed part, whereas their connecting plate is in the shape of a tender,

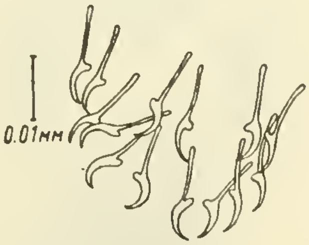

Fig. 177. *Bychowskyella pseudobagri* Achmerow, attaching armature of a free-swimming larva.

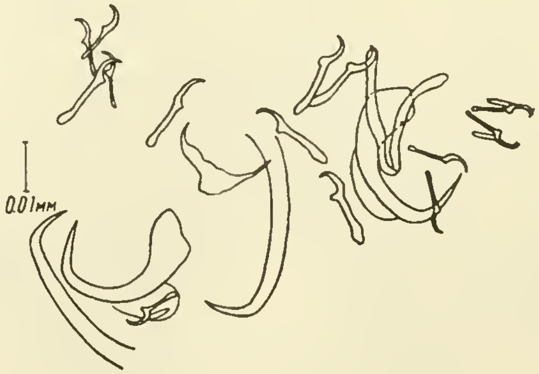

Fig. 178. *Bychowskyella pseudobagri* Achmerow, attaching armature of the young worm in the process of development. *Pseudobagrus fulvidraco* (Rich.). (According to Gussew, 1955).

V-shaped, curved chitinous membrane and finally large edge hooks already forming handles" (see Fig. 178). Consequently we see that the development of *Bychowskyella* takes place in the same fashion as among *Ancylodiscoides* Yamaguti with the exceptions of differences in the development of the edge hooks.

8. The development of *Heteronchocleidus* Bychowsky

Heteronchocleidus buschkieli Bychowsky (Fig. 118), which was studied by us from aquarium fishes, is a representative of curious tropical monogenetic trematodes, which are related to the family Dactylogyridae (Ancyrocephalinae), parasitizing Anabantidae. The internal structure is of the usual type for this family, the presence in the adult stage of three fully developed middle hooks and one (hook, *nobis*) which is very retarded in development, and many times smaller in size than the rest (Fig. 179) is characteristic for them. The embryonic development takes place within 5 to 6 days. The free-swimming larva of *H. buschkieli* (Fig. 180) corresponds to that of representatives of the genus p. 165
Ancyclodiscoides. Its length is about 0.07 mm and its width is 0.02-0.03 mm. The ciliary covering consists of a zone divided into two groups with a weakly developed middle and a larger undivided third. The larva has 14 very tender edge hooks on its disc which are about 0.009 mm in length. In addition, somewhat above them, lies the first pair of middle hooks in the shape of slightly curved little parentheses of slightly greater length than the lateral hooks (0.009 - 0.011 mm) (they are not expressed on the drawing because of their unusual frailty). The connecting plate of the first pair and the second pair of middle hooks are still absent. The

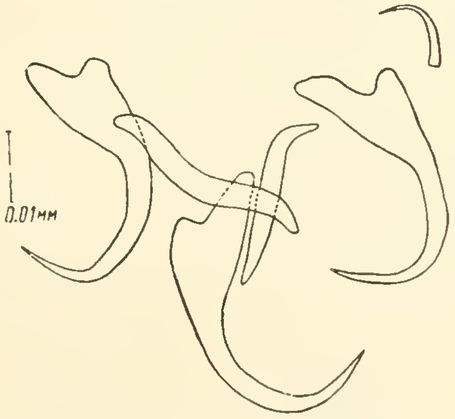

Fig. 179. *Heteronchocleidus buschkielli* Bychowsky, attaching armature of the disc of an adult worm from the gills of little aquarium fish *Macropodus opercularis* (L.) Leningrad.

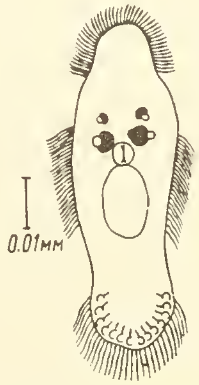

Fig. 180. *Heteronchocleidus buschkielli* Bychowsky, free-swimming larva.

development of the attached larva apparently proceeds in the usual way (unfortunately this has not been fully studied). It is known only that one hook of the first pair of middle hooks does not grow at all in the post-embryonic period. During the early stages of development this hook (during the observation on live worms) acts completely normally and serves, just as the one corresponding to it, for the attachment of the larva, whereas among adult individuals it doesn't play any role whatsoever.

9. The development of Diplectanum Diesing

As is known, the genus Diplectanum (Fig. 14) is characterized by the presence of a more complex attaching armature than among all the previous genera. The attaching apparatus (Fig. 56) consists of 14 lateral hooks, 2 pairs of middle hooks, 3 connecting plates--one unpaired middle and 2 paired, articulated with the middle hooks, and finally of 2 peculiar supplementary discs, all deployed on the disc. These discs (whence comes the name of the genus) lie on the upper edge of the attaching disc one on the ventral and one on the dorsal side and are equipped with a large number of small chitinous stick-shaped formations with hook-shaped offshoots located in regular rows (Fig. 181). The development of the genus unfortunately has not been studied; known are only the free-swimming larvae of D. aculeatum Parona and Perugia and D. similis Bychowsky, a new species which is very close to the first species and of which we collected a large number of individuals in June 1935 at the Sebastopol Biological Station and in July-August 1949 at the Karadaga Biological Station from the eggs deposited by worms on the Gorbil (Corvina nigra Cuv. and Val.) (Humpback Salmon, nobis). p. 166
These larvae resemble those of the genus Dactylogyrus but deserve detailed description. The free-swimming larvae (Fig. 182) which have just emerged from the egg have an elongated, torpedo-shaped form with blunt anterior ends and a very sharpened posterior end. At the anterior

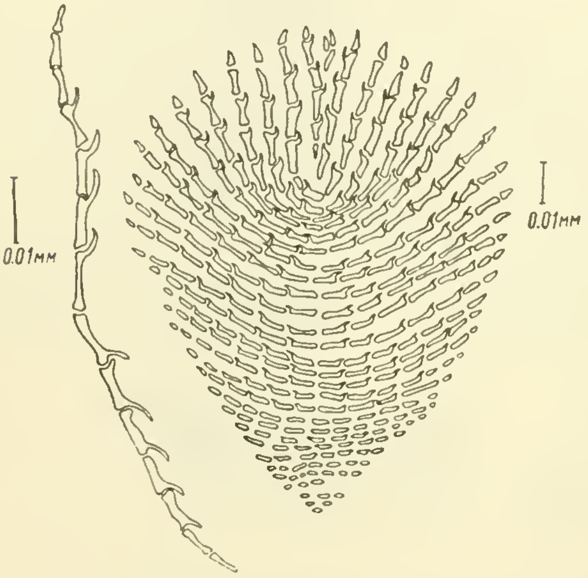

Fig. 181. Diplectanum aculeatum Parona and Perugia, chitinous armature "plectans" of an adult worms from the gills of Corvina nigra Cuv. and Val. from the region of Karadaga (Black Sea). On the left is one row, greatly magnified.

end of the larva there is a small, rather mobile nose-shaped growth, and approximately at the end of the second third of the body, there are small indentations which delineate the weakly differentiated attaching disc. In D. aculeatum Parona and Perugia the length of the larva (in the straightened condition) is 0.07 to 0.10 mm, whereas the width is 0.03 - 0.04 mm and among D. similis Bychowsky the length is 0.06 - 0.08 mm and the width is 0.03 - 0.35 mm. The ciliary covering consists of three zones. Its anterior zone is located on the head end and extends posteriorly to the level of the anterior pair of eye spots. It is divided by the nose-shaped growth into two lateral groups of cells and on the ventral side they are closely separated from each other, whereas on the dorsal side they merge at the middle line of the body. The second zone of ciliary epithelium is located along the sides of the body in two parts, which extend posteriorly from the level of the pharynx to the anterior edge of the attaching disc. Both groups of this zone extend to the ventral and dorsal sides of the body but do not touch each other. The third zone, consisting of two groups merging with each other, is located behind the attaching disc on a cone-shaped growth of considerable dimensions (among both species about 0.008 - 0.012 x 0.012 - 0.015 mm). This growth is exceedingly mobile and serves in some measure for the regulation of the direction of the motion of the larva. This cone is completely discarded as a unit with the shedding of the ciliary epithelium when the larva becomes attached to the host. The larva carries two groups of glands with well-developed ducts at the head end. There are two pairs of large eyes (the anterior are somewhat smaller) with large light-refracting lenses facing outside from the pigmented spot. The pharynx lies behind the eyes, it is round and about 0.015 mm in diameter; the intestine is sac-shaped, weakly developed and poorly noticeable. During the study of live subjects one can observe the lateral trunks of the excretory system which give off numerous outgrowths and form a number of anastomoses. Between the eyes and the anterior end of the pharynx two transversal canals depart from the lateral trunks of the excretory system. These canals merge in the middle and proceed toward the anterior end where they separate dichotomously. It has not been possible

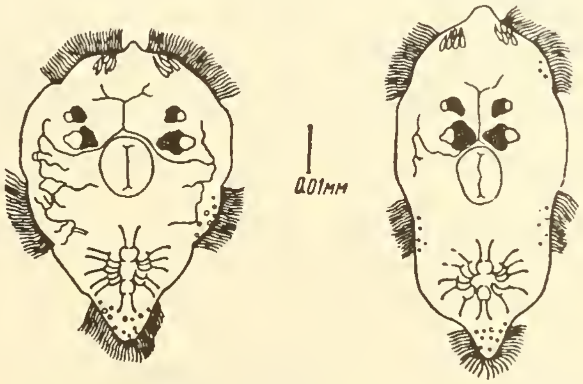

Fig. 182. Diplectanum silimis Bychowsky, free-swimming larvae.

to ascertain the number of flame cells; however, it can be said that their number is considerably larger than 20. The sizes of these cells are about 0.005 mm. The attaching disc is sharply delineated from the rest of the body and is somewhat smaller in width. The armature of the disc consists of 14 edge hooks of the usual shape for Dactylogyridae with a length of about 0.012 mm among *D. aculeatum* and about 0.008 mm among *D. similis*. In such a fashion, all four middle hooks, three connecting plates, and both attaching plates are incepted and developed already after the attachment of the larvae to its host. p. 167

10. The development of *Lamellodiscus* Johnston and Tiegs

The genus *Lamellodiscus* (Fig. 34) is very close to *Diplectanum* Diesing and differs mainly in that its supplementary discs carry not a number of stick-shaped formations but a number of concentrically disposed chitinous threads (Fig. 183). During our work at the Karadaga Biological Station in July-August, 1947 we obtained free-swimming larvae of two species (*L. elegans* Bychowsky, and *L. fraternus* Bychowsky) and studied the development of one of them more in detail. The material for this work was collected from the gills of *Sargus annularis* (L.).

The free-swimming larvae of both species emerge from the eggs three or four days after the deposition of the latter by the mother individual. The larvae are torpedo-shaped just as the larvae of *Diplectanum* which they greatly resemble both in exterior shape and interior structure (Fig. 184). The sizes of the larvae of both species are the same: their length is about 0.09 mm with a width of 0.03 mm (the

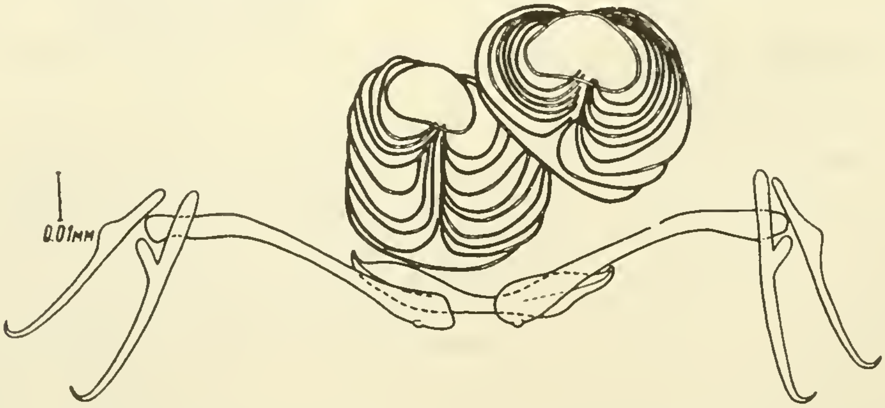

Fig. 183. *Lamellodiscus elegans* Bychowsky, middle hooks, their connecting apparatus and chitinous armature of the supplementary discs of an adult worm from *Sargus annularis* (L.) from the region of Karadaga (Black Sea).

greatest width is at the level of the first or second pair of eyes); the attaching disc is almost round, about 0.025—0.028 mm across; the dimensions of the pharynx are about 0.01 - 0.008 mm. The attaching armature consists of 14 edge hooks 0.008 - 0.011 mm in length. The ciliary epithelium of the larva is cast off at different times. One can often observe the settled larvae with a part of the ciliary cells which have been retained. The latter fall off in groups, at first on the attaching disc and the anterior end of the body. The cone-shaped growth, on which the third zone of cilia is located, falls off as a unit as is evident from p. 168
Figure 184.

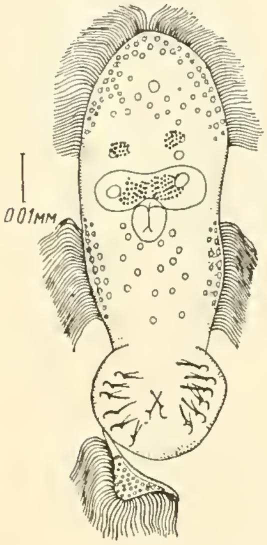

Fig. 184. Lamellodiscus fraternus Bychowsky, free-swimming larva casting off the cone of the ciliary zone of the posterior end.

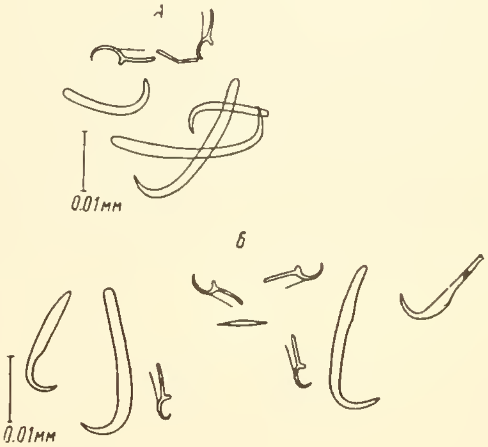

Fig. 185. Lamellodiscus elegans Bychowsky, attaching armature of the disc of the larva in the process of development from the gills of Sargus annularis (L.) from the region of Karadaga (Black Sea). Explanation in text.

Strange as it may seem the larvae which have just settled are somewhat smaller in size in comparison with the free-swimming stage. Thus, the youngest larvae which are discovered on the gills of the host. have the length of 0.06 - 0.07 mm and a width of 0.025 - 0.035 mm. They begin to feed very quickly and their attaching disc acquires the transversly elongated shape characteristic for the genus. The edge hooks stop growing completely and retain their initial sizes during the entire life of the worms. The middle hooks begin to form almost simultaneously and grow quickly. At first they have the shape of weakly curved plates of the same width for their entire length with a sharply bent and sharpened lower end--the point of the hook (Fig. 185, A). Somewhat after the inception of the middle hooks the central connecting piece appears in the form of a straight or slightly curved and hardly noticeable little plate (Fig. 185, B).

The disposition on the disc of these attaching formations is not uniform. In the free-swimming larvae the edge hooks, which lie along the edge of the disc with their points facing the ventral side, retain their location, with the exception of the first two pairs which unfold and lie with their edges toward the dorsal side. This disposition of edge hooks persists during their entire life among worms of this genus. The large pair of middle hooks, i.e., first from the point of view of time of inception is located on the ventral side but is oriented with its points toward the dorsal side, whereas the smaller pair, which is closer to the dorsal side, conversly faces the ventral side with its points. The unpaired middle connecting plate is incepted and lies on the ventral side. The following stage of development of *L. elegans* (Fig. 186) is characterized p. 169 by the appearance of inceptions of the paired connecting plates. They appear on the dorsal side along the edges of the middle plate and have the shape of straight sticks, sharpened toward the middle line of the disc, and slightly widening toward the opposite end. They are incepted in the interior of the parenchyma of the disc without touching the chitinous elements on either side. During this stage of development the length of worms is about 0.08 mm whereas the width is about 0.035 mm; the attaching disc is about 0.045 mm in width.

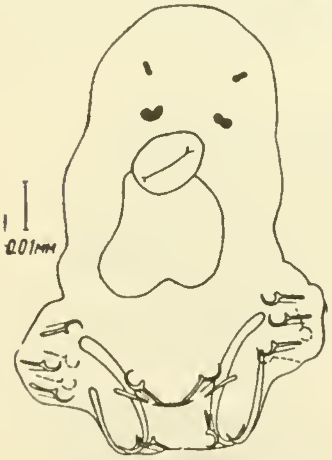

Fig. 186. *Lamellodiscus elegans* Bychowsky, young worm from the gills of *Sargus annularis* from the region of Karadaga (Black Sea).

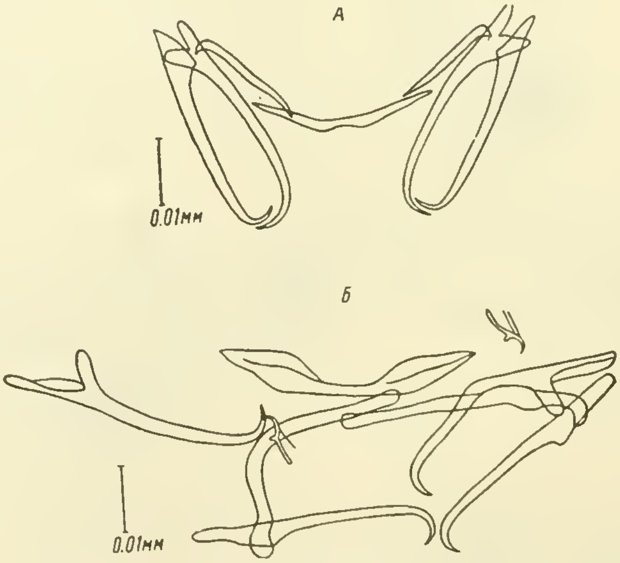

Fig. 187. *Lamellodiscus elegans* Bychowsky, attaching armature of the disc of developing worms from the gills of *Sargus annularis* (L.) from the region of Karadaga (Black Sea). Explanation in text.

At that time the digestive system has grown considerably but the intestine still has a sac-like form. At this stage of the division the sizes of the pharynx are about 0.017 - 0.012 mm, i.e., considerably larger than among the free-swimming larvae even though the dimensions of the worm are still approximately equal those of the larva. As was described before, the edge hooks do not grow but remain about 0.008 - 0.011 mm in length. The middle hooks have the following lengths: the first pair about 0.03 mm, the second 0.02 mm, the middle connecting plate 0.012 - 0.014 mm, and the lateral, paired 0.008 - 0.01 mm in length. The further development of the attaching armature proceeds rather intensively. It is characterized by a rapid growth of middle hooks and of the connecting plates which acquire their difinitive shape and sizes (Fig. 187, A) before the beginning of the formation of the attaching plates on the disc. The growth of the middle hooks proceeds as among all preceding species by way of the accretion of the end which is opposite to the point. The connecting plates increase mainly by way of growth on both ends, at the same time they thicken throughout their lengths (Fig. 187, B).

The following stage of development is characterized by the formation of both supplementary discs (Fig. 188). They are incepted simultaneously on the dorsal and ventral side and at first are hardly p. 170

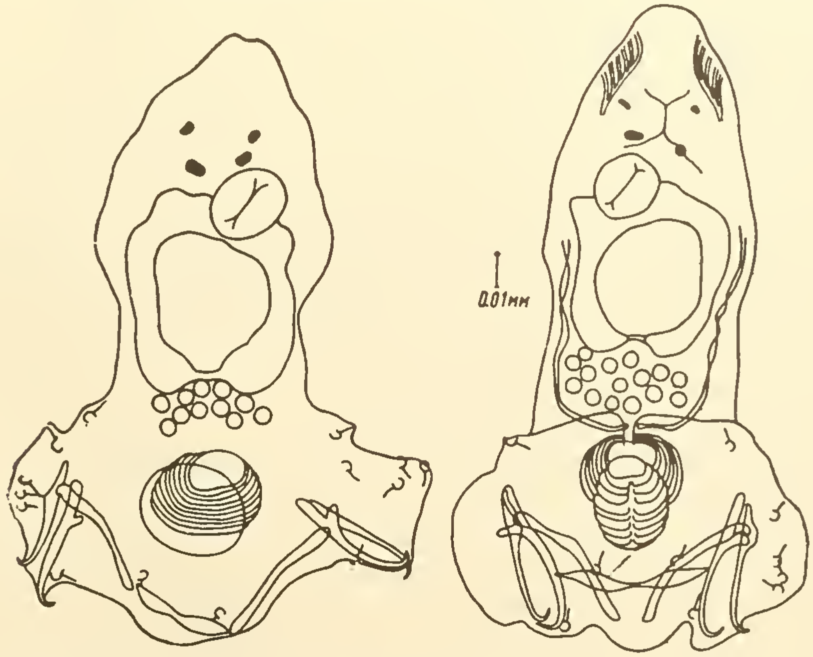

Fig. 188. Lamellodiscus elegans Bychowsky, young worms from the gills of Sargus annularis from the region of Karadaga (Black Sea); stages of the beginning of development of the supplementary discs.

noticeable. However, the inception of these formations takes place in such a way that all their elements are formed at the same time and then gradually grow and thicken. During this stage the digestive system already has its final circular shape, but the sex system has not yet been completely developed. The approximate sizes of the worms during that stage are: length 0.11 - 0.13 mm, width 0.04 - 0.07 mm; length of the disc 0.05 - 0.06 mm with a width of 0.08 - 0.09 mm; the pharynx is about 0.025 x 0.020 mm; the length of the first pair of middle hooks is 0.043 - 0.046 mm and of the second pair 0.038 - 0.040 mm; that of the middle connecting plate about 0.045 mm; and of the lateral plates 0.045 - 0.047 mm; the sizes of the supplementary discs (at rest) 0.03 x 0.035 mm.

The further development takes place mainly by way of the formation of the sex system and the strengthening of the structures of the attaching apparatus which serve for the articulation of the middle plates with each other and the middle hooks. Considerable growth of the worms, which increase almost three times in length in comparison with the stages just described and which already have a fully developed attaching apparatus, takes place during this time. One must also note that the inception of the copulatory organ takes place almost directly after the formation of the attaching plates and the sex system begins to function and the worms deposit eggs much before reaching their final sizes.

11. The development of *Calceostomella* Palombi p. 171

In contrast to all preceding genera, *Calceostomella* is characterized by the fact that during the attachment of the adult individual the basic significance is acquired by the attaching disc itself and not its armature which is developed so weakly that until the present time it was not even really known whether the edge hooks exist, or if they exist what is their number. As our studies of *C. inerme* Parona and Perugia have shown, the attaching armature of this species corresponds to that of Dactylogyridae and consists of 12 typical edge hooks and two middle hooks. The adult *C. inermis* (Fig. 189) differ by a strongly developed glandular fringe of the anterior end of the body, by relatively large testes and strong development of vitellaria which almost fill the entire body of the animal. The copulatory organ is chitinous, with powerfully developed prostatic glands. The development of representatives of the genus has not been studied. We obtained a free-swimming larva of *C. inermis* at the Sebastopol Biological Station (on the fifth day after the deposition of eggs); during July, 1935 the worms which were collected from the Gorbil (*Corvina nigra* Salv.) (Humpback Salmon, *nobis*) intensively deposited eggs. The larva which emerged from the egg is cigar-shaped and has a length of about 0.1 mm and a width of 0.03 mm. The ciliary epithelium is well-developed and of the usual disposition. The eyes number 2 pairs and are relatively large and are located in front of the pharynx. The attaching disc is already sharply separated from the rest of the body in the larvae which emerges from the egg. The interior organization of the larva is the same as in *Dactylogyrus*. The attaching armature (Fig. 190) is represented by 12 lateral hooks and 2 middle hooks p. 172 which have the characteristic shape with already developed interior and exterior offshoots. The sizes of edge hooks are 0.012 - 0.014 mm, the sizes of the middle ones are 0.010 - 0.011 mm. During subsequent development the middle and edge hooks stop growing and among the adult individuals they have the same dimensions. We shall also indicate that during the time of development the growth of the eyes does not take place and it is possible that among the adults they are reduced (disappear? *nobis*) because we were not able to find traces of eyespots among certain adult individuals.

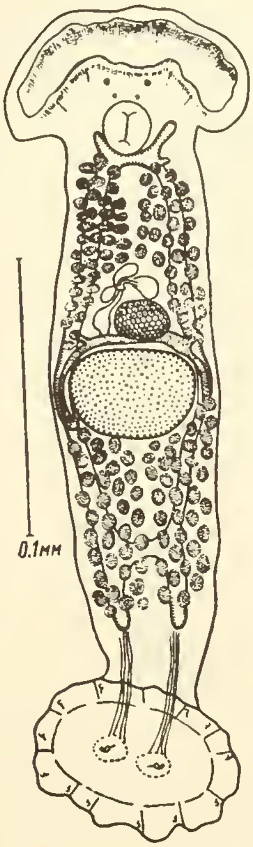

Fig. 189. *Calceostomella inermae* (Parona and Perugia), young worm from the fins of *Corvina nigra* Salv. from the Bay of Naples (Mediterranean Sea).

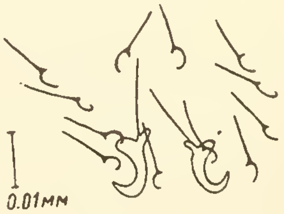

Fig. 190. *Calceostomella inermae* (Parona and Perugia), attaching armature of a free-swimming larva.

12. The development of *Tetraonchus* Diesing

Among the representatives of the genus *Tetraonchus* (Fig. 64) the presence of 4 eyes, of a pipe-shaped intestine and of an attaching disc with 16 edge and 14 middle hooks is characteristic; the latter are linked with each other by a single connecting plate.

In August of 1949 on the Island of Hanka, A. V. Gussew hatched a considerable number of larvae from the eggs of *T. monenteron* (Wagener) which parasitize the gills of *Esox reicherti* Dyb. The development of larvae within the eggs continued about 3 to 4 days. A number of the hatched larvae were impregnated with silver. We also hatched larvae of *T. monenteron* (Wagener) from the eggs of worms from *Esox lucius* L.

studied in the Delta of the Volga (June, 1954). The development of the eggs took place approximately with the same speed as on the Island of Hanka and the emergence of the larvae was observed on the third day. The material obtained was also partially impregnated with silver. Further description is based upon the study of the preparations from both regions.

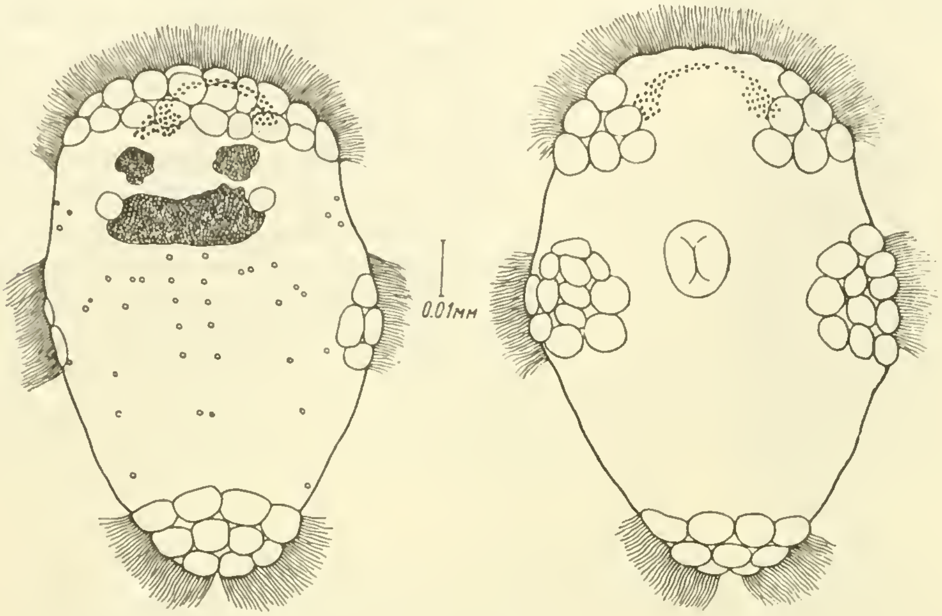

Fig. 191. Tetraonchus monenteron (Wagener), location of ciliary cells of the body of a free-swimming larva. The larva on the left is in dorsal view, and on the right in ventral view. Impregnated with silver.

The larvae which emerged from the eggs have the customary elongated form. Their length is about 0. 12 mm with a width of 0. 04 mm; in fixed state they are somewhat shorter--0. 08 - 0. 10 mm long with a width of 0. 06 to 0. 07 mm. The ciliary covering is located in three zones. In the silvered specimens (Fig. 191) it is evident that each zone consists of a p. 17
different number of large, rounded cells (with a diameter about 0. 005 mm). The anterior zone lies basically on the dorsal side from the very edge of the body and reaches posteriorly to the level of the first pair of eyespots The edges of the anterior zone extend to the ventral side where they terminate, reaching not further than the corresponding eyespot on each side, and in such a fashion the middle of the ventral surface of the anterior edge of the body is deprived of ciliary covering. The total number of cells of the anterior zone equals approximately 32, of which 18 lie on the dorsal side and 6 on each side of the ventral. In opposition to the preceding anterior one the middle zone of ciliary cells lies mainly on the ventral side, only partially extending to the sides of the body. It consists of two sections (about 14-15 cells), which start from the level of the pharynx and extend posteriorly somewhat further than the edge of the first half of the body of the larva. Both sections of the ciliary cells of the middle zone

occupy a lateral location, and between them a bare space remains on each side of the body which is considerably larger on the dorsal side and smaller on the ventral side. The posterior zone occupies the entire end of the body and is somewhat more powerfully developed on the dorsal side. The number of cells which compose it is about 17 of which 10 lie on the dorsal side. All in all the ciliary covering of the larva consists of 61 to 62 cells.

The attaching disc of the larva is almost not delineated from the body; it bears 16 edge hooks of the typical shape for the genus (Fig. 192), 0.010 - 0.012 mm in length. Each hook is equipped with a well-developed little loop and a thin tendon. In addition to the edge hooks, two little parentheses of 0.007 mm in length, which apparently represent the inceptions of the first pair of middle hooks, are visible somewhat closer to the anterior end of the body. These little parentheses are not visible in all preparations and have very indefinite contours, consequently we hesitate to state with conviction that they are middle hooks.

The inner organization of the larva in preparations has not been sufficiently studied. Strongly developed eye spots are clearly apparent. There are three of them--one pair of the anterior and one large posterior spot fused from two halves, which is equipped with light refracting little lenses on both sides. The anterior eyes have a diameter of about 0.005 mm whereas the posterior eye is about 0.01 mm in length and has a width of 0.03 mm. The light-refracting little lenses are about 0.003– to 0.004 mm in diameter. The pharynx which lies behind the posterior eye is slightly elongated (sagittally, *nobis*) and is about 0.015 to 0.017 by 0.012 to 0.014 mm in size. The inception of the intestine is not visible in the larva. Further development is not known. Among the larvae impregnated with silver, attention is drawn by several strongly light-refracting bodies (with a diameter of about 0.001 mm) the edges of which are blackened with silver, these are symmetrically distributed in the body (close to its dorsal side). Their number is very considerable (more than 40) but it is not possible to say what they are without further special study.

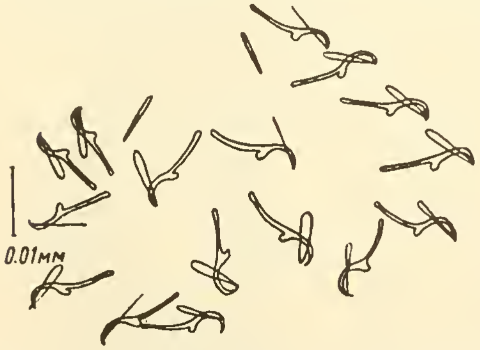

Fig. 192. *Tetraonchus monenteron* (Wagener), attaching armature of a free-swimming larva.

13. The development of Tetraonchoides Bychowsky

The curious species, T. paradoxus (Fig. 29) was described by us recently from Uranoscopus scaber L. It is characterized by a pipe-shaped intestine and a complex attaching apparatus with four supplementary sucker-shaped growths on the dorsal surface of the attaching disc. The armature of the latter participates in attachment but the main role is played by the powerful attaching disc itself. In 1935 at the Sebastopol Biological Station we obtained free-swimming larvae of this species, but unfortunately the drawings of these larvae were lost. From the notes and indications in our work (Bychowsky, 1937) it is apparent that the larva is devoid of eyes just as are the adult individuals. It has a sac-shaped intestine and only 16 edge hooks on the well-developed attaching disc. Thus the formation of the remaining attaching armature in this species takes place in the postembryonic period. p. 174

14. The development of Nitzschia Baer

The representatives of the genus Nitzschia (Fig. 17) have two attaching grooves on the head end and a powerfully developed sucker-shaped disc at the posterior end. The armature of the disc consists of 14 edge and 3 pair of middle hooks; there are no septa on the interior surface of the sucker-shaped disc. The sex system is strongly developed and the testes are very numerous. The sex oriface opens on the ventral side of the body almost along its middle line. They parasitize sturgeons.

We studied the development of N. sturionis Abildgaard in July, 1932 during our work on the Caspian Sea (Island of Sara). The larvae were obtained from eggs deposited by individuals collected from the great sturgeon--Huso huso (L.). The Nitzschia larva which has just hatched from the eggs has an elongated cylindrical body, but with slightly thickened ends and a slightly inflated middle and three zones of ciliary epithelium (Fig. 193). Its length is about 0.35 mm and the width is 0.1 mm. The anterior end of the larva has two clearly expressed thickenings equipped with a number of glands corresponding to the head growths of Dactylogyrus and the attaching organs of the head ends of Epibdella and Benedenia. Directly behind these thickenings are located 2 pairs of large eyes under which, closer to the ventral side of the body, lie 2 large head ganglia of the nervous system. The ciliary covering of the head end of the larva starts from the anterior edge and terminates at a level with the posterior end of the anterior pair of eyes. The pharynx of rounded shape and relatively large dimensions is located somewhat away from the eyes; a small ring-shaped intestine emerges from the pharynx. The second zone of ciliary epithelium starts at the level of the middle of the intestine. It is located mainly along the sides of the body and terminates near the beginning of the attaching disc. The excretory system is easily noticeable;

its effering openings, located along the sides of the body, are somewhat displaced toward the dorsal side, and are located at the level of the beginning of the second zone of ciliary covering. The structure of the excretory system was not followed through by us but it is completely evident that its longitudinal trunks are doubled on each side. Immediately upon its emergence from the egg, the attaching disc of the larva is well-developed and separated from the body, and all its edges are drawn toward the middle, and at that time it is incapable of functioning. The armature of the attaching disc (Fig. 194) consists of 14 edge hooks and 3 pairs of middle hooks of p. 175
different shapes and sizes just as among adult worms. The attaching disc bears a third zone of ciliary epithelium which starts somewhat at the front of the middle of the disc and terminates at its posterior end. The attaching armature deserves special description. The edge hooks have uniformly straight handles and a comparatively powerful transversal growth of the terminal little hook. Their sizes are more or less the same, their length fluctuates from 0.019 - 0.021 mm just as among adult individuals. The first pair of middle hooks which is located near the lower posterior edge of the disc, has the shape of the middle hooks of Dactylogyrus which are just completing the growth of the basal part. Their sizes are about 0.03 mm. The second pair is located behind the first somewhat away from the center of the attaching disc. In its shape it is an elongated plate with an obliquely-growing upper edge and slightly curved lower edge ending in a somewhat obtuse, rounded "point." The sizes of the second pair are considerably larger-- 0.048 - 0.050 mm. Finally, the third pair, located almost in the center of the disc of the larva, have the shape of hooks with a slightly widening basal part and with an almost straightened point and lateral offshoot which lies between the point and the basal part and has a somewhat curved and free end which is directed toward the same side as the point.

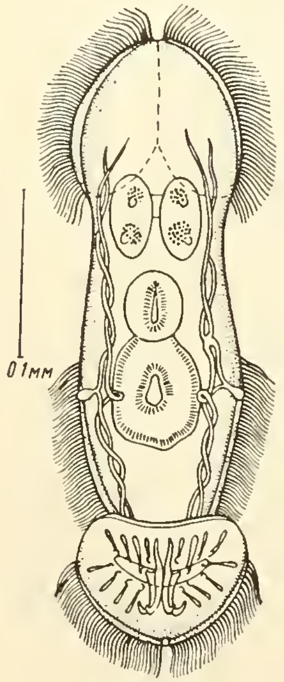

Fig. 193. Nitzschia sturionis (Abildgaard), free-swimming larva.

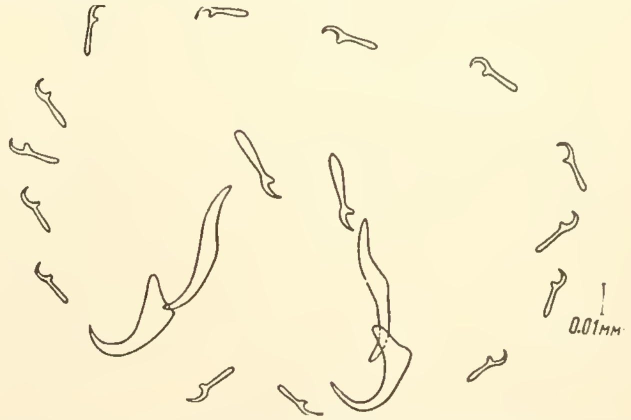

Fig. 194. Nitzschia sturionis (Abildgaard), attaching armature of a free-swimming larva.

Generally this hook closely resembles the edge hooks in structure. The sizes of middle hooks of the third pair are about 0.034 - 0.036 mm. After a relatively small interval of time after emergence of the larva from the egg, the edge and the middle hooks of the attaching disc "cut through," i.e., their edges protrude outside, while the disc itself unfolds and the larva acquires the ability for attachment. A gradual change of the larva into the adult stage takes place after the attachment to the body of the host and the shedding of the ciliary epithelium. The head thickenings change into the so-called attaching grooves, and the sex p. 176 system is developed and the nervous and excretory systems grow and acquire their final form. The pharynx grows quickly and becomes barrel-shaped, whereas the intestine develops and forms a number of lateral branches. Finally, the attaching disc strongly increases in dimensions and acquires the shape of a powerful sucker. As has already been indicated, the edge hooks do not grow, whereas the middle ones not only grow very intensively but also change their form. The growth of the middle hooks takes place differently (Fig. 195). The first pair grows approximately 4 to 5 times and the growth takes place, as in all middle hooks of the usual type, by way of accretion at the free end of the basal part. The larval hook remains in such a fashion as an unchanged lower part of the hook. The second pair also grows approximately 4 to 5 times, but this growth is different. Here takes place not only accretion at the free end but also a general thickening so that the exterior, lower edge of the hook of the adult individual corresponds to the hook of the larva. Finally, the third pair grows approximately 4 times and growth develops in all directions although in a larger measure in the basal part than near the edge so that although the hook greatly changes in shape it nevertheless remains bifurcated in the lower part just as in the larva.

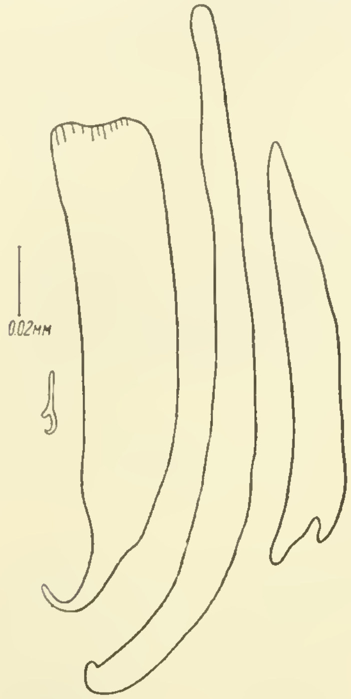

Fig. 195. *Nitzschia sturionis* (Abildgaard), attaching armature of an adult worm from the buccal cavity of *Huso huso* (L.) near the Island of *Sara* (Caspian Sea).

A few words about the biology of the larvae. According to our observations, the attachment of the larvae by their anterior ends to various underwater objects takes place only when the attaching disc functions fully; until that time the larva only feels the encountered obstacles.

The experiments which we conducted show that immediately upon emerging from the egg, the larva of *Nitzschia* possess a strong positive phototaxis and only with the unfolding of the disc does it change into the negative one, in complete conformity with the behavior of the larva of *Dactylogyrus* which was described by us. At the beginning of their lives the larvae swim with unusual speed and force. Upon hatching from the eggs in saltshakers (stender dishes or test tubes?, at least some type of experimental container, *nobis*) they immediately "fly out" from them breaking through the film of the surface tension of the water and sliding along the dry surface of the glass for almost a centimeter above the water. The larvae retain the ability to infest the host fro 5 to 6 hours and after that they lose it although they remain alive and swim in the water approximately 24 hours.

15. The development of *Benedenia* Diesing

The genus *Benedenia* (Fig. 196) appears to be the typical representative of Capsalidae. It is characterized by a powerful development of the two head suckers and the attaching disc. The latter is equipped on its inner surface with septa which divide the disc into one central and 7 edge p. 177 sections. The chitinous armature of the disc consists of 14 edge and 6 middle hooks. The internal structure of the representatives of this genus is uniform: There is a well-developed intestine with a large number of exterior and interior branches. The sex system has two large testes and a large ovary and the effering ducts open at the sides of the body.

In 1932, Jahn and Kuhn described the development of *B. melleni* MacCallum, a parasite of American marine fishes, in considerable detail. Then we studied the development of a second species--*B. derzhavini* (Layman) from the gill cavity of *Sebastodes schlegeli* (Hildendorff) in Vladivostok in June, 1949. For the convenience of comparison of the data obtained we shall first give the information concerning the development of *B. melleni* in the form of a somewhat abbreviated translation from the work of the authors enumerated above and then the data themselves.

We must say that we have changed the terminology of Jahn and Kuhn somewhat in line with that accepted by us in the present work.

"The free-swimming larva of *B. melleni* (Fig. 197) is about 0.23 mm in length and 0.06 in width, it is flattened at the anterior end and spindle-shaped at the base with the exception of a narrowing in the region of the buccal opening. The posterior one-third of the larva forms an attaching disc which does not function when the larva emerges and which has the sides folded together. The pharynx is rounded, muscular and p. 178 located in the anterior part of the middle third of the body. It opens into a very short esophagus which changes into two relatively large intestinal trunks which extend almost to the end of the body. There are no lateral outgrowths.

There are two pairs of eyes in front of the buccal opening on the dorsal surface of the body. They are in the form of cup-shaped masses of pigment, in a cavity of which lie spherical hyaline lenses. The lenses of the posterior pair of eyes are approximately 0.016 mm in diameter and lie in front of and to the side of the pigmented cups. The lenses of the first pair are 0.012 mm in diameter and lie posteriorly and to the side. The head suckers, which are not fully developed, have the shape of padded sections easily visible in live individuals. The excretory system (Fig. 199) is represented by two relatively large excretory bladders located somewhat behind and laterally to the buccal opening, with 4 canals leading from them, and 10 pairs of flame cells. The excretory system opens in dorsal pairs just as among adult forms. There are 2 large excretory canals[1] each starting from the

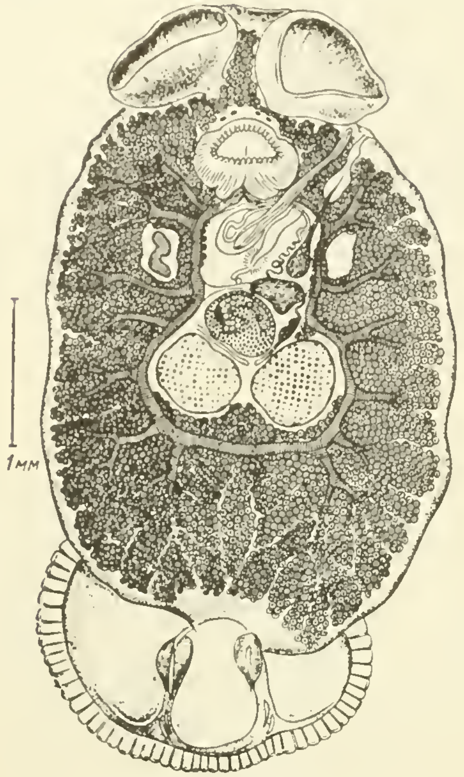

Fig. 196. Benedenia derzhavini (Lajman), adult worm from the interior surface of the operculum of Sebastodes schlegeli (Hilg.) near Vladivostok (Sea of Japan)

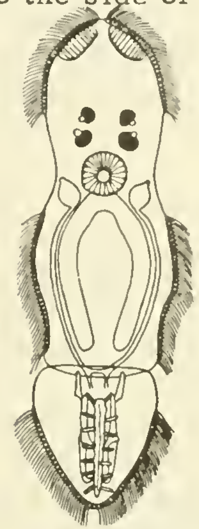

Fig. 197. Benedenia melleni (MacCallum), free-swimming larva. Natural size 0.23 mm. (According to Jahn and Kuhn, 1932).

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[1] One must suppose that the description of the authors regarding the number of lateral canals is not accurate because the presence of two basic canals on each side is characteristic for the majority of monogenetic trematodes in which the excretory system has been studied.

corresponding bladder and extending posteriorly into the attaching disc. They are connected by a transversal vessel in the posterior part of the body. Each of these canals gives off one branch oriented forward which terminates by one flame cell lying approximately in the middle between the excretory bladder and the transversal vessel. The longitudinal canals extend into the sucker and branch off into five vessels each in the latter. These vessels terminate in flame cells. In addition to the large canals a smaller one leading to the anterior end of the body emerges from each of the excretory bladders. They unite in front of the buccal opening and form p. 179 the middle canal which leads forward between the eyes, beyond which it divides and branches off to the sides. Further, each one of the branches bifurcates anteriorly and posteriorly and the branches thus formed terminate in flame cells. There are four more flame cells in the region of the buccal opening lying in front and behind the pharynx. Their canals apparently branch off from the anteriolateral (canal, nobis). Thus, the arrangement of the excretory ducts of the larva amounts to a "circular" system with two lateral pores. The excretory system has a similar structure in adult individuals. The larva is equipped with cilia in the anterior, middle and posterior parts of the body. The anterior ciliary zone extends in front of the first pair of eyes and the cilia practically cover the entire anterior part of the body with the exception of the cephalic attaching organs. The middle ciliary zone starts from the posterior end of the excretory bladders and extends to the posterior end of the body (up to the disc) and covers the sides and the lateral, dorsal and ventral surfaces with cilia. There are no cilia in the middle of the dorsal or in the middle of the ventral surfaces. The posterior ciliary zone occupies the lateral and dorsal surfaces of the

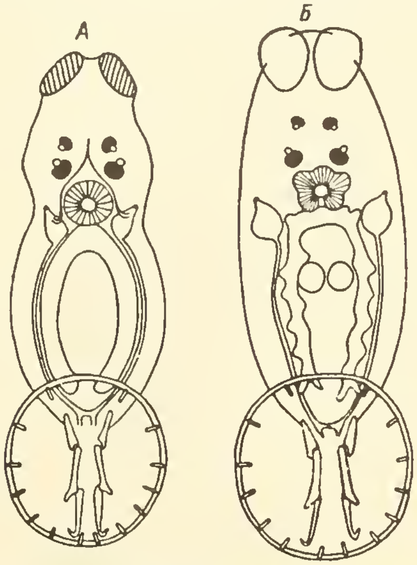

Fig. 198. Benedenia melleni (MacCallum), stages of the development of the larva. Explanation in text. (According to Jahn and Kuhn, 1932).

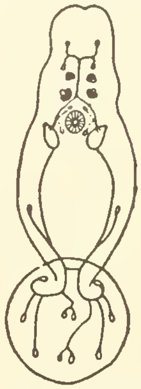

Fig. 199. Benedenia melleni (MacCallum), diagram of the excretory system of the free-swimming larva. (According to Jahn and Kuhn, 1932).

posterior two-thirds of the attaching disc. The cilia are relatively long and form from a special epithelium which is clearly visible in live samples. The loss of cilia and ciliary epithelium takes place simultaneously. The attaching disc is folded during the time of the swimming of the larva; it is equipped with middle hooks characteristic for all adult individuals. These hooks lie longitudinally in such a way that their curved ends are located mesially and are visible on the ventral side. The edges of the folded little sucker lie ventrally from the middle hooks and are equipped with lateral hooks. The latter are of equal length, approximately 0.01 mm in length. In live individuals the cephalic attaching organs are very mobile, they even attach themselves to the container in which the larvae are located, and even draw up the entire body behind them. The loss of the ciliary epithelium begins soon after the appearance of this ability. Usually the ciliary covering of the anterior and posterior zones are lost first. The attaching disc unfolds at the same time as the shedding of the epithelium (Fig. 198, A). When it has completely unfolded the middle hooks turn along their long axes and their curved ends protrude outside whereas the lateral hooks are disposed radially along the edge of the attaching disc. At that time the attaching disc already begins to function and attaches to the container. When the larva finds a host, in the beginning it probably attaches by means of the head organs and only afterwards by means of the disc, more precisely by means of its 14 edge hooks and perhaps by means of the posterior pair of the middle ones. After the attachment of the larva (Fig. 198, B) the first noticeable morphological changes are expressed in the transformation of the attaching head organs into the final head suckers. Further, the pharynx which is rounded in the larva acquires the lobed shape very characteristic for the adults. The intestinal trunks begin to put out lateral growths. The diameter of the attaching disc is relatively large in relation to the body. Its middle hooks increase in size and change their form, whereas the lateral do not change and do not grow. Because of this we can deduce that they do not have any significance in the adult form. Further development is expressed mainly in the development of the digestive system and the increase of the excretory system and particularly in the development of the sex system. The size of the eyes in the larva and among the adult is approximately the same. Only their location which is trapezoid-shaped is different among the adults. One must also note that the growth of the (middle hooks of the, nobis) attaching disc proceeds unequally so that at the end of the period of growth the size p. 180 of the middle and anterior pairs is more than six times larger than of the same ones among young worms, whereas the posterior pair increases only three times" (Jahn and Kuhn, 1932).

The free-swimming larvae of *B. derzhavini*, which have just emerged from the eggs on the 10th day after their deposition are very similar to the larvae of *B. melleni*, but differ in a number of peculiarities. Their sizes are somewhat larger and the correlation of their parts is different. The length of the larvae is about 0.26 mm and the width in the middle of the body about 0.07 mm. The body is torpedo-shaped (Fig. 200), rather narrowed at the level of the pharynx and in front of the attaching disc. The latter is well-developed, it is sharply delineated from the rest of the body, and rather larger than among B. melleni. Among free-swimming larvae it is somewhat elongated in length. Its sizes are about 0.09 - 0.08 mm. The head end is slightly flattened, the ducts of the head glands open into it by bunches. The latter are rather powerfully developed and lie along the sides of the body between the posterior pair of the eyes and the pharynx. There are no "pad-shaped" sections from which, according to Jahn and Kuhn, suckers are formed. In its structure the anterior end completely corresponds to the one among Dactylogyridae, the only difference being that the number of head ducts in B. derzhavini is larger and their size is more considerable. The eyes, which have the usual location, are powerfully developed. The anterior pair is one and one-half times smaller than the posterior in diameter. The lenses of the eyes are large and often of oval form. The digestive system is well-developed. The pharynx is rounded and has a diameter of about 0.03 mm; from it extends, clearly visible in the live subjects, a sac-shaped intestine which exceeds the diameter of the pharynx by three to four times. In such a fashion the structure of the intestine in our species sharply differs from the one among B. melleni. The excretory system is poorly studied. Two powerful flask-shaped excretory bladders, the dimensions of which exceed the diameter of the pharynx, depart from (open outside by, nobis) the dorsal pores. Two excretory trunks emerge anteriorly and posteriorly from the bladders (see note on page 178). These canals lie just as they are pictured by Jahn and Kuhn in B. melleni with certain deviations indicated on the drawing. We did not succeed in counting the number of flame cells, but it is considerable. The ciliary covering of the larva is analogous to the one in B. melleni, but the description of Jahn and Kuhn seems inaccurate to us. The anterior zone lies away from the anterior end of the body at a certain distance and extends posteriorly to the level of the first pair of eyes. It not only leaves the places of the efferring ducts of the head glands free, but it is also interrupted on the ventral and dorsal sides. The middle zone begins below the excretory bladders and extends up to the disc and apparently forms a break on the ventral side, whereas it extends fully on the dorsal side. The third zone occupies the posterior half of the

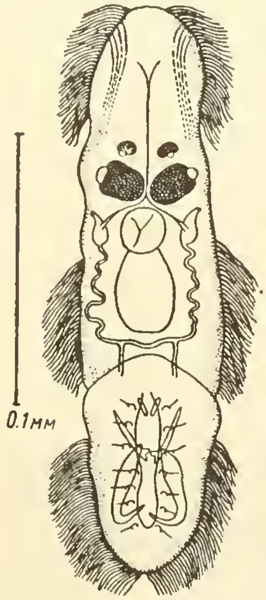

Fig. 200. Benedenia derzhavini (Lajman), free-swimming larva.

attaching disc but forms a small break on the very posterior end on which a small, hill-shaped growth is located. Altogether the ciliary covering of the larva carries evident traits of bifurcation into right and left independent halves. The casting off of the ciliary epithelium takes place unequally: the p. 181 middle zone is shed last. The attaching armature (Fig. 201) of the larva consists of 14 edge hooks and 3 pairs of middle hooks. The edge hooks are 0.012 - 0.015 mm in length. They are of the usual dactylogyrid-form with a handle of constant thickness in its entire length. The sizes of the edge hooks do not change during the entire life of the worms. The first pair of middle hooks lies near the posterior end of the attaching disc. They have the shape of the middle hooks of Dactylogyridae with undeveloped offshoots resembling the hooks of Nitzschia but relatively more massive. The length of this pair in D. derzhavini is about 0.028 - 0.03 mm. The second pair of middle hooks lie somewhat closer to the center of the attaching disc, leaning with the lower half against the first. The hooks of this pair resemble the middle hooks of the lowest groups with a basal part which is long but compressed at the sides and rounded on its free end and changing on the opposing end into a small, sharply-curved point. Along with this,a small sharpened offshoot, as if it were a small second point, departs at the place of its determined beginning along the exterior curvature of the hook in the opposite direction. The length of the hook of the third pair is about 0.038 - 0.04 mm. The third pair of middle hooks lies almost at the center of the attaching disc and has the shape of little sticks bifurcated at the lower end

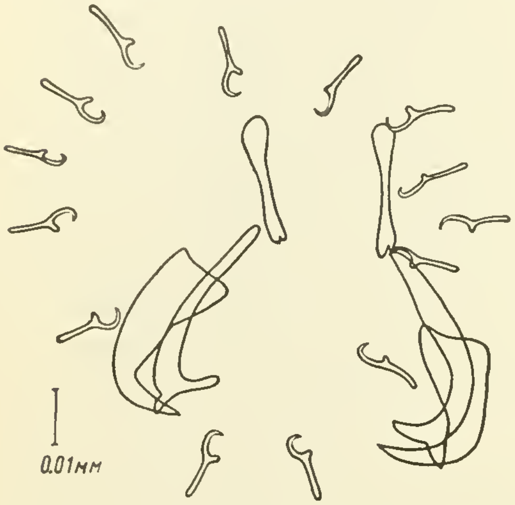

Fig. 201. Benedenia derzhavini (Lajman), attaching armature of a free-swimming larva.

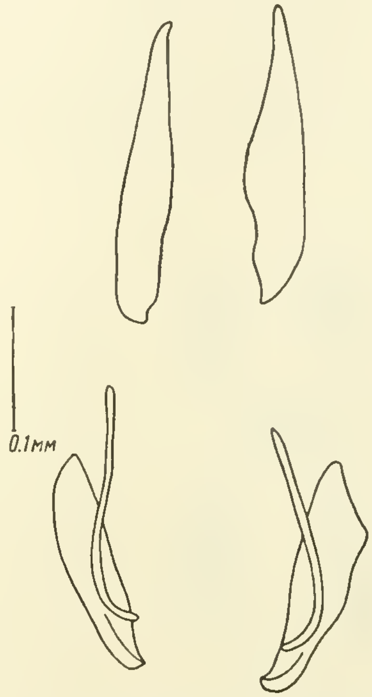

Fig. 202. Benedenia derzhavini (Lajman), middle hooks of an adult worm from the gill cavity of Sebastodes schlegeli (Hilg.) near Vladivostok (Sea of Japan).

and rounded at the upper end. The hooks of this pair are very similar to the corresponding ones in Nitzschia. Their sizes are 0.026 - 0.028 mm. In their description of the development of B. melleni, Jahn and Kuhn do not indicate that the growth of the middle hooks is accompanied by changes in their shapes. In B. derzhavini they are considerable which is apparent from the comparison of the middle hooks of the larvae with those of the adult animals (Fig. 201 and 202). The growth of the separate pairs of the p. 182 middle hooks is also unequal in B. derzhavini; thus the first pair increases in length about 6 times, whereas the second about five times and the third 9 times. Thus the tempo of growth and its correlation among middle hooks of both types of Benedenia which were studied is completely different. The development of the larvae until the adult stage is analogous to the one which we saw in Nitzschia sturionis Abildgaard and Benedenia melleni (MacCallum)

16. The development of Polystoma Zeder

We have at our disposal materials on the development of three species: P. integerrimum Froelich, P. nearcticum (Paul), P. ozaki Price. A number of authors studied P. integerrimum (Zeller, 1872a, 1876; Halkin, 1901; Goldschmidt, 1902a, 1902b; Gallien 1932a, 1933, 1934b, 1935). It was studied with a considerable degree of completeness starting from cleavage. From the fall of 1927 until the fall of 1929 we also conducted research on the development and life cycle of P. integerrimum, which unfortunately remains unpublished. We shall note that P. integerrimum is characterized in the adult stage by the presence of 6 suckers on the attaching disc which also serve for the attachment of the animal. The chitinous armature of the disc, which exists among adult worms, either does not play any role at all in attachment (edge hooks) or an extremely insignificant role (middle hooks). As is known, there are two mature forms in the life cycle of P. integerrimum: one which grows slowly and parasitizes the urinary bladders of frogs, while the other, with a quick tempo of development lives in the gill cavity of the tadpoles. Taking into consideration that both of these forms, have, in addition, a different morphology (Figs. 22, 127) one could expect

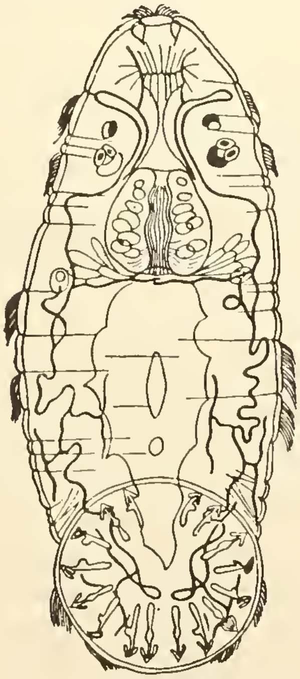

Fig. 203. Polystoma integerrimum Froelich, free-swimming larva. Natural size about 0.3 mm. (According to Halkin, 1902).

the presence of two different types of larvae which would develop from eggs deposited by these different forms. However, actually the free-swimming larvae which have just emerged from the eggs of gill *Polystoma* do not differ morphologically from those from the eggs of polystomes which parasitize the urinary bladder. The eggs of *P. integerrimum* are deposited in the water and the cleavage takes place already in the external medium, among the individuals from the urinary bladder just as among forms from the gill cavity. The free-swimming larva of *P. integerrimum* is more complexly organized than all the preceding forms, mainly by way of the increase of the ciliary covering and its greater differentiation, and of the separate parts of the body. The larva (Fig. 203) has an elongated body shape which slightly narrows toward the anterior end, and also has a well-expressed attaching disc. The latter is folded in the beginning and then unfolds after a very short period following the emergence of the larva from the egg. The sizes of the larvae are relatively large: the length is about 0.3 mm and the width is about 0.07 - 0.09 mm. The p. 183 ciliary covering is distributed in three zones (Fig. 204) just as among the previous types; however, these zones have a more complex structure and lie not only along the sides of the body but extend also to the dorsal and ventral surfaces. For the study of details of the location of the ciliary covering of *P. integerrimum* we, together with T. Tsiborskayia, a colleague of our laboratory, conducted a special research in which we utilized the method of silvering widely accepted for the study of the

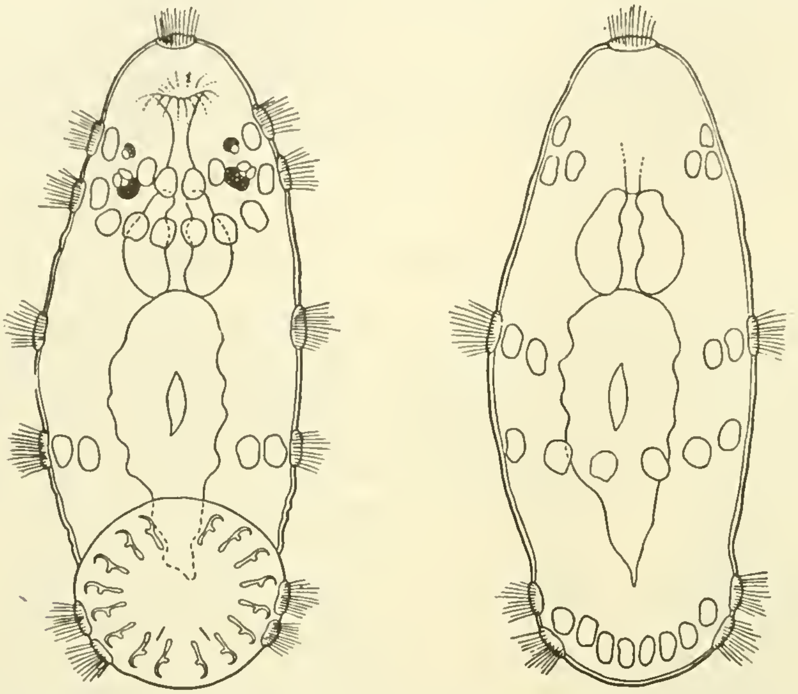

Fig. 204. *Polystoma integerrimum* Froelich, the location of the ciliary cells on the body of a free-swimming larva. Left in ventral, and right in dorsal view. Impregnation with silver. Schematically.

simplest forms and which has already been applied to Monogenoidea (see page 187). First of all,our data affirmed that the number of cells of ciliary epithelium among larvae of Polystomatidae is constant as was supposed earlier and first determined by Ozaki (Ozaki, 1935b). Altogether the ciliary epithelium of the larvae of *P. integerrimum* consists of 55 cells. It is characteristic that the cells of the ciliary epithelium do not form a continual covering but each of them lies separately (lie in separate zones, *nobis*). The first zone of ciliary cells is located in front of the first pair of eyes and consists of 25 cells located (symmetrically in relation to the mesial line of the body) in two groups. The first group consists only of one cell which lies terminally or more often is slightly displaced to the dorsal side; the 18 cells of the second group are located on the ventral side as a belt completely encompassing that side of the body of the larva, whereas the remaining 6 cells of this group are located on the dorsal side with three on each side so that the basic part of the dorsal surface is deprived of ciliary epithelium. The second zone consists of 18 ciliary cells divided into two groups, of which the first lies approximately at the level of the middle of the pharynx and the second somewhat toward the front of the anterior end of the attaching disc. The first group has 6 cells p. 184
located on the dorsal side, three on each side of the body so that the edge cells are easily visible from the ventral side of the larva. The first group of this zone consists of 12 cells lying symmetrically in a group of 6 cells on the ventral and dorsal sides. Finally, in the third zone, 12 cells lie on the dorsal side of the posterior half of the attaching disc somewhat away from its posterior end so that the 2 edge ones on each side are clearly visible from the ventral side when the larva is observed. In such a fashion 24 ciliary cells are located on the ventral side of the larva, while on the dorsal--30, and finally one cell lies terminally. Apparently such an unequal distribution of cells appears to be the reason for the peculiar swaying motion of the free-swimming larva.

The head end of the larva is equipped with four groups of glands. Four pigmented eyes of the larva with well-expressed lenses are located somewhat in front of the pharynx. The digestive system is rather powerfully developed. The pharynx is somewhat extended in length (0.04 x 0.035 mm), it lies at the end of the first and the beginning of the second third of the body. The intestinal tract emerges from it in the form of a small esophagus. The intestinal tract is elongated, with 2 branches which merge in the end of the body. Between the 2 branches of the intestine there is one, or more rarely, 2 anastomoses lying approximately in the middle part of the intestinal space. The excretory system is well-developed. Its openings are located along the sides of the body and on the dorsal side and somewhat behind the pharynx. There are also small excretory bladders. The trunks of the excretory system, which lead to the posterior and anterior ends of the body on each side, apparently do not form transversal connecting canals. One must note that we ourselves did not study the excretory system, and all the existing descriptions and drawings of it among P. integerrimum are too schematic. The attaching armature of the disc of the larva is represented by 16 edge hooks and a pair of middle hooks (Fig. 205). The edge hooks are of the typical shape with a well-expressed transversal growth between the terminal hooks and the handle. The middle hooks have the shape of small chitinous little parentheses of smaller sizes than the lateral hooks. The length of the edge hooks is 0.028 - 0.032 mm and of the middle hooks 0.018 - 0.02 mm.

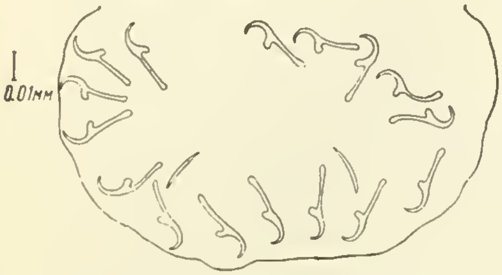

Fig. 205. Polystoma integerrimum Froelich, attaching disc of a free-swimming larva. Strongly compressed.

After its attachment to the gills of the host and loss of the ciliary epithelium the fate of the larva is twofold. In the case of accelerated growth, the formation of the gill form (see page 121 and Fig. 127), its metamorphosis is accompanied by intensified feeding, in connection with which the intestine grows considerably. The latter acquires sac-like form with vague outgrowths along the exterior edge and a few interior anastomoses. The posterior end of the intestine extends into the attaching disc and even occupies a large part of it. The sex system of the type different than the one which parasitizes the urinary bladder develops quickly. Its basic peculiarities are: a strongly elongated and p. 185 sausage-shaped ovary; the absence of vaginal ducts and of the ductus genito-intestinalis; the absence of the uterus proper and the presence only of the ootype in which the eggs are formed one at a time; and finally the presence of one testis of a rounded form. The attaching disc grows unequally. The lateral hooks remain without change in shape and size, whereas the middle hooks grow relatively little reaching 0.04 - 0.045 mm in length, and do not form any offshoots. Subsequently starting from the posterior end of the disc, suckers are incepted at the places of 3 pairs of lateral hooks (6th, 5th, and 4th) in such a fashion that the lateral hooks eventually are located in the centers of the sucker. For the most part, the sizes of the suckers remain unequal during the entire life of the worm, the posterior are larger and the anterior are smaller. The attaching disc is often strongly deformed and has an irregular shape, depending to a great degree on the size and nature of the gill cavity of the host. Among the larvae which develop into the adult form in the urinary bladder the development takes place much slower and the worms reach their final structure only in the second year of their life in contrast to the gill forms all the development of which takes place within a few weeks. The larva begins its metamorphosis on the gills of the tadpoles succeeding largely in forming the first and second pair of suckers. It is true that these suckers do not as yet have the final form and dimensions (Fig. 206, A and B). At the same time with the metamorphosis of the tadpoles and the loss of the gills by them, the larva of *P. integerrimum* passes through the intestinal tract to the urinary bladder where it finally settles. The last pair of the suckers of the larva Fig. 206, C) develop in the urinary bladder and it terminates its metamorphosis. The growth of the individual continues during its entire life, i. e., about 4 to 5 years, whereas maturity is reached at the end of the second year. The attaching disc of *Polystoma* of the urinary bladder is well-expressed and delineated from the rest of

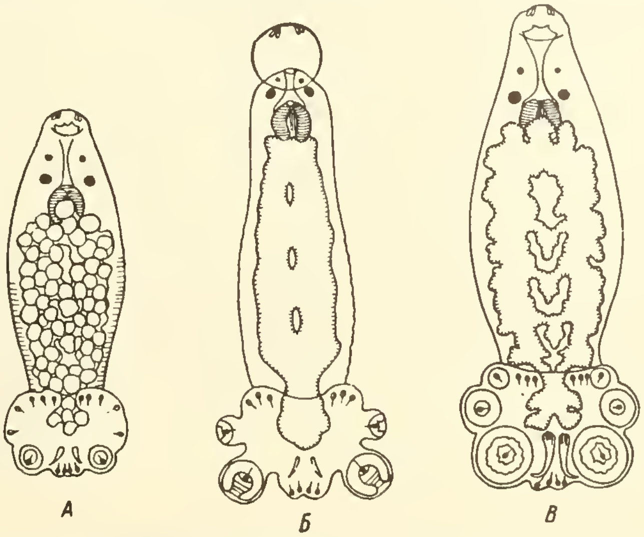

Fig. 206. *Polystoma integerrimum* Froelich, stages of metamorphosis of the larva. Explanation in text. (According to Zeller, 1872).

the body from the very beginning of its development. Just as among the gill form,the edge hooks do not grow, whereas the middle hooks reach p. 186
considerable sizes,forming both offshoots and apparently grow during the greater part of the life of the individual (at any rate after it reaches maturity). Suckers are formed around the same pairs of lateral hooks but have a more regular shape and already at the end of the first year they have the same sizes while continuing, at the same time, to grow for a relatively long time. The intestinal tract acquires its final shape, with three characteristic internal anastomoses by the end of the first year of life. The sex system differs from the one of the gill individuals by a more compact structure of the ovary and the presence of the ductus genito-intestinalis, 2 vaginal ducts, an elongated uterus capable of holding more than two dozen eggs, and with a large follicular testis. It is interesting that the structure of the copulatory organ in both forms is identical; also identical in form and number are the hooks which are located as a wreath at the base of the penis.

The development of *P. nearcticum* (Paul) was studied by the author of the species (Paul, 1938) and it is very similar to the one of *P. integerrimum*. It is interesting that the gill form is also discovered in this species which means that this is not an exclusive peculiarity of P. integerrimum but is common to the entire genus or at any rate to a number of its representatives.

P. ozaki Price apparently has a similar development to P. integerrimum but with a more delayed tempo. This type resembles the first extremely closely but differs by a powerful development of the digestive system. We have observed the process of metamorphosis of the larva of this species in the young frog (Rana chensinensis Dov.) on southern Sakhalin in the regions of Antonov in 1946. The larvae reached the urinary bladder of the frog at earlier stages than among P. integerrimum, i.e., while they do not even have the first pair of suckers.

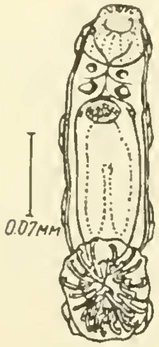

Fig. 207. Polystomoides oris Paul, free-swimming larva. (According to Paul, 1938).

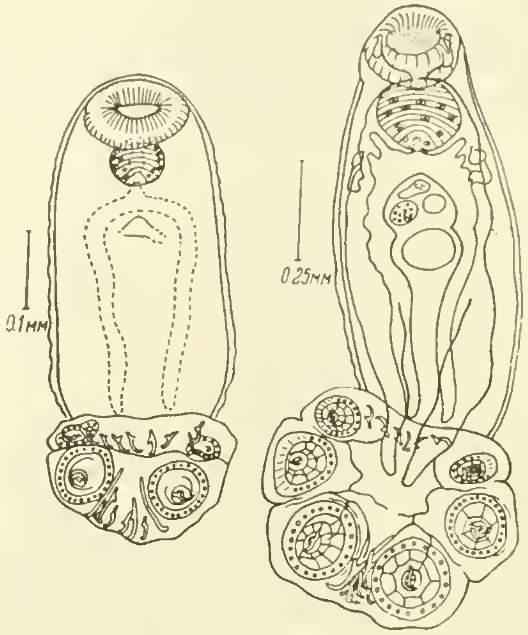

Fig. 208. Polystomoides oris, Paul, two stages of development of the young worms from the buccal cavity of the turtle Chrysemys picta (Schneider). (According to Paul, 1938).

17. The development of Polystomoides Ward

p. 187

The genus Polystomoides is characterized by the presence of one large testis, by the absence of a uterus (there is only an oötype), and by simple, unbranched intestinal trunks (Fig. 82). Paul (Paul, 1938) worked on the development of P. oris Paul from the buccal cavity of Chrysemys picta (Schneider). The larva develops in the eggs for approximately 28 days. Upon emergence from the egg it swims freely, thanks to the four zones of ciliary epithelium (Fig. 207). The structure of the larva is very similar to that of the representatives of the genus Polystoma. Its sizes are 0.275 by 0.065 mm. The attaching disc bears 16 pairs of edge hooks and 2 pairs of middle hooks of which one pair is larger. The sizes of edge hooks do not change in the process of further development of the larva and remain about 0.03 mm during the entire life. The smallest pair of middle hooks in the larva is 0.035 mm and grows among adult worms up to 0.065 mm. Finally, the larger pair changes its sizes from 0.035 to 0.12 mm. The fate of the larva which reaches the buccal cavity of its host where the adult worms live is poorly studied; however, in general traits its development apparently is analogous to that of Polystoma (Fig. 208).

18. The development of Diplorchis Ozaki

The genus Diplorchis is also close to that of Polystoma but differs by simple unbranched intestinal trunks, the presence of 2 testes, and by the very powerful development of the uterus which extends posteriorly to the attaching disc, filling the middle part of the body of the worm almost fully, and almost completely displacing the parenchyma and the vitellaria beyond the intestinal trunks.

Ozaki (Ozaki, 1935b) worked on the development of D. ranae Ozaki. He observed the deposition of eggs and also gave a good description of the free-swimming larva. The eggs of D. ranae begin to develop in the uterus of the parent individual. The eggs which are deposited contain fully formed larvae (Fig. 209). The free-swimming larva which emerges from the egg which is already in the water has a cigar-shaped, elongated form (Fig.210). Its length is 0.24 - 0.28 mm and its maximum width is about 0.08 - 0.1 mm. Its widest part is between the anterior end and the pharynx; its anterior end is rounded, the attaching disc is well-delineated. The ciliary covering of the larva of D. ranae (Fig. 211) was studied by Ozaki by means of the silver impregnation technique. Thus,the precise distribution and numbers of ciliary cells was clarified. Their total number is 59. The cells are distributed in 5 groups lying symmetrically on the ventral and dorsal surfaces and extending to the lateral edges. The first group consists of one cell on the anterior, terminal end of the body of the larva. The second consists of 26 cells located in a continuous mass on the ventral surface of the larva from the buccal opening posterior to the first half of the pharynx. The third group is located at the level of the posterior edge of the pharynx and extends somewhat behind. It consists of 3 pairs of cells along the sides of the body of the larva. The fourth group is located near the posterior end of the body and consists of 12 cells forming a little belt along the dorsal side and the edges of the body and extending only slightly onto the ventral surface. Finally the fifth group consisting of 14 cells is located on the sides and the dorsal surface of the posterior half of the attaching disc. Comparing the ciliary covering of D. ranae with that of Polystoma integerrimum we see an almost

p. 188

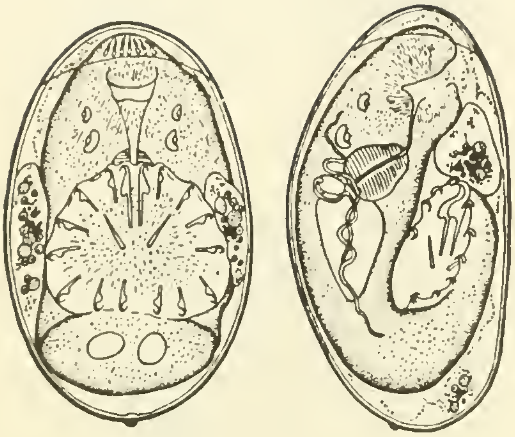

Fig. 209. Diplorchis ranae Ozaki, ripe eggs with formed larvae. (According to Ozaki, 1935).

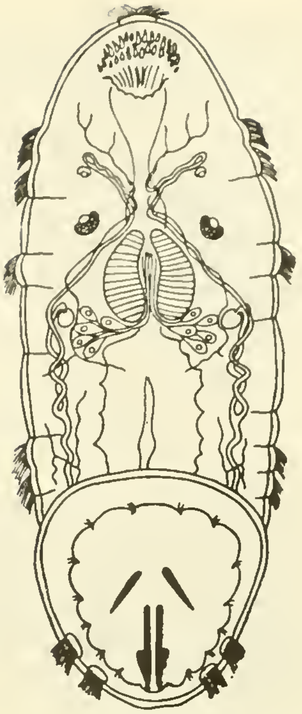

Fig. 210. Diplorchis ranae Ozaki, free-swimming larva. (According to Ozaki, 1935).

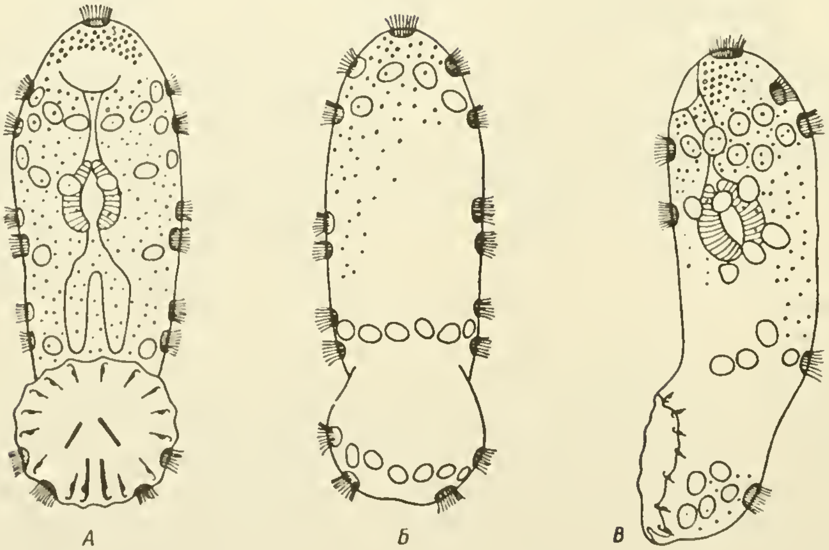

Fig. 211. Diplorchis ranae Ozaki, location of ciliary cells on the body of free-swimming larva. A--In ventral view; B--In dorsal view; C--In lateral view. (According to Ozaki, 1935).

complete resemblance although the number of cells in *P. integerrimum* is somewhat smaller and their location is such that we prefer to speak of three and not five zones of ciliary epithelium. There is no doubt that the 5 zones of cells in *D. ranae* represents the next step in the differentiation of the ciliary epithelium. This is seen especially clearly in the examination of *D. ranae* from the dorsal surface (Fig. 211). For we can observe from that view the rapprochement between the first and second, third and fourth groups of ciliary cells, i.e., their three-zoned distribution.

There are 2 pairs of pigmented eyes located at the end of the p. 189
first third of the body. The digestive system is represented by the barrel-shaped pharynx located posteriorly to the eyes, by a short esophagus and two intestinal trunks which end blindly without extending into the attaching disc. The excretory system (Fig. 212) of *D. ranae* was studied by Ozaki fairly accurately. It is of the same type as among *Polystoma*. It is well-developed. The excretory openings lie dorsally along the sides of the body at the level of the esophagus. The attaching armature (Fig. 213) is represented by 16 lateral hooks lying along the edge of the disc and by 2 middle hooks. The lateral hooks are of the same type as among *Polystoma*, but are of two sizes. The first 7 pairs are small, 0.017 - 0.02 mm in length and the 8th pair is almost twice as large—0.034 - 0.038 mm. The middle hooks have the shape of straight needles, slightly thickened near the lower terminal; their length is 0.022 - 0.027 mm. Further development of *D. ranae* has not been studied but apparently proceeds as among *Polystoma*. The presence of a gill form is unknown.

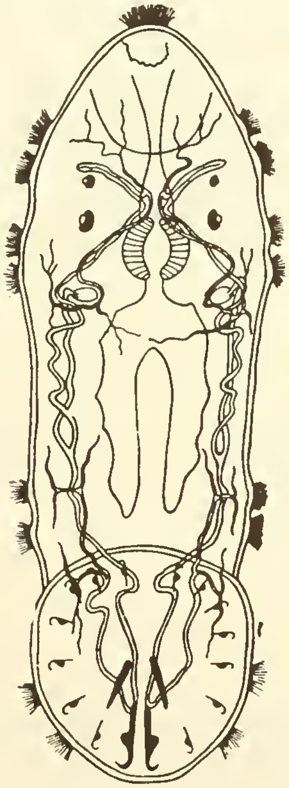
Fig. 212. *Diplorchis ranae* Ozaki, excretory system of a free-swimming larva. (According to Ozaki, 1935).

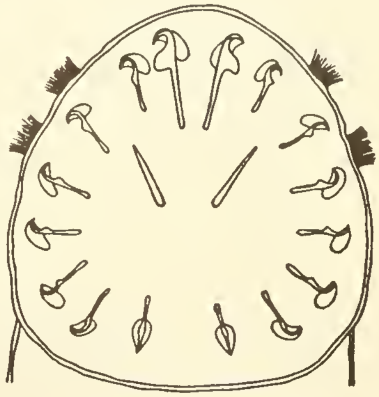
Fig. 213. *Diplorchis ranae* Ozaki, attaching armature of the disc of the free-swimming larva. (According to Ozaki, 1935).

In 1941 Rogers (Rogers) described a new species of Diplorchis (D. scaphiopi) from the frog, Scaphiopus bombifrons Cope (United States of America, Oklahoma), and gave a short description and schematic representation of the free-swimming larva of that species. Judging from the data of Rogers the larva of D. scaphiopi hardly differs from the larva of D. ranae Ozaki.

19. The development of Neopolystoma Price

p. 190

In the summer of 1949, U. A. Strelkov, a collaborator of our laboratory, studied N. palpebrae, a parasite of the far-eastern turtle Amyda sinensis (Wieg.), which he described in 1950 (Fig. 50). This species appears to be a typical representative of the genus; the latter was characterized by Price (Price, 1939) as being very close to Polystomoides and Polystomoidella but differs from them in the absence of middle hooks. Development in the eggs of N. palpebrae takes place in 24 days. The larva which emerges from the egg (Fig. 214) is apparently covered with a continuous very small and tender ciliary covering. U. A. Strelkov and A. V. Gussew, who together observed the free-swimming larvae, indicated that the ciliary covering of N. palpebrae is scarcely noticeable; in the beginning it even seemed to them that the larvae were completely devoid of ciliary coverings. The larva has the usual shape for the Polystomatidae; its length is about 0. 3 mm and its width is about 0. 1 mm. The attaching disc is rounded, sharply delineated from the rest of the body and has a diameter of about 0. 08 mm. The larva has four eyes located in the customary places, the digestive system consists of a

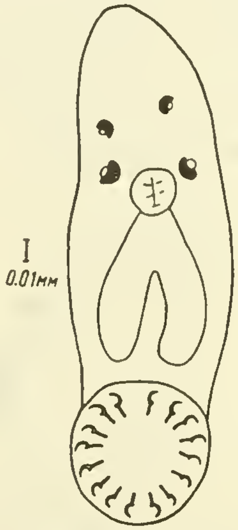

Fig. 214. Neopolystoma palpebrae Strelkov, the larva of which emerge from the egg (ciliary covering ?), strongly compressed.

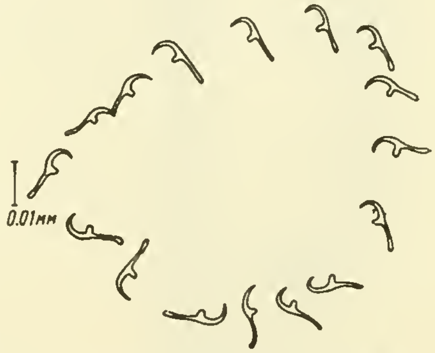

Fig. 215. Neopolystoma palpebrae Strelkov, attaching armature of the larva which has just emerged from the egg.

rounded pharynx about 0.03 mm in diameter and two intestinal trunks which end blindly. The esophagus is practically absent or very short. The excretory system was not observed. The attaching armature of the disc (Fig. 215) consists of 16 edge hooks of the usual form for Polystomatidae and of the same length--0.015 mm. According to the observations of U. A. Strelkov and A. V. Gussew the free-swimming larva moves relatively slowly and begins to stop rather quickly and to "feel" the bottom of the container. The method of infection of turtles and the further development of N. palpebrae are not known.

20. The development of Sphyranura Wright p. 191

The structure of the trematodes of the genus Sphyranura,
which parasitize the gills of Necturus, is very odd. In addition to the
peculiarities of the structure of the sex and digestive systems, adult
worms of this genus (Fig. 35) are characterized mainly by the structure
of the attaching apparatus. The latter is represented by a well-developed
disc bearing 2 powerful suckers, 16 edge hooks, of which two lie in the p. 192
center of the suckers, and 2 large middle hooks (Fig. 216).

In 1936 Alvey studied the development of Sph. oligorchis Alvey, although in our opinion not thoroughly enough. The development of eggs took place in the external medium during a prolonged period of time. Alvey removed the developing larvae from the eggs from the 26th day of development and then obtained free-swimming larvae emerging from the egg on the 27th to the 29th days (Figs. 217 - 218) and finally studied them after attachment. The indications of the author that the larvae are almost completely deprived of ciliary covering are very strange because according to his own observations they are very mobile and swim with the help of their disc (?!). We think that actually the

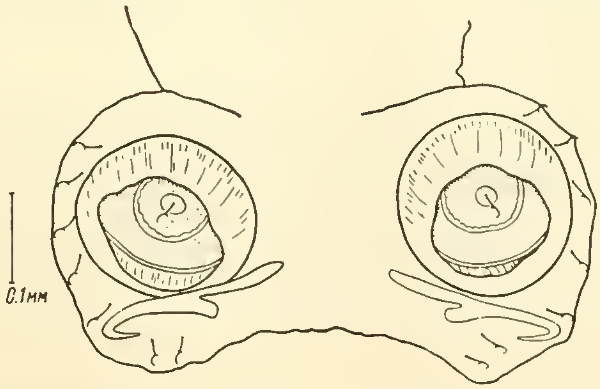

Fig. 216. Sphyranura osleri Wright, attaching disc of an adult worm from the gills of Necturus sp. from the Huron River (Michigan, U.S.A.)

larvae of Sph. oligorchis has a ciliary covering of the same type as Neopolystoma palpebrae which the author was unable to find. The larvae emerge from the egg with a greater or lesser development of the attaching armature and of its separate parts (Fig. 219), but they already have the same relations of the disc and armature as the grown forms, i.e., edge hooks of the final size, 2 middle hooks and 2 suckers. The middle hooks and both suckers do not have the final form or dimensions and grow for a long period of time. The sizes of the edge hooks of the larva are about 0.25 mm, the length of the middle hooks is about 0.011 mm[1]. The internal organization of the larva was poorly studied by the author. It is known that there is a more or less well-developed pharynx and a small circular intestine. The eyes are absent just as among adult worms. The excretory bladders lie along the sides of the intestine and are easily noticeable in the larva. The development of the sex system takes place, according to Alvey, in about 2 months.

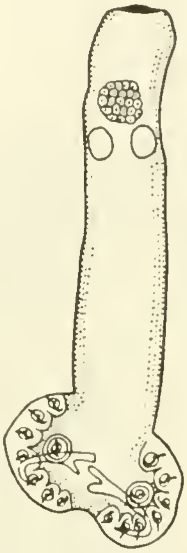

Fig. 217. Sphyranura oligorchis Alvey, larva which emerge from the egg on the 27th day of development. Magnified 188 times. (According to Alvey, 1936).

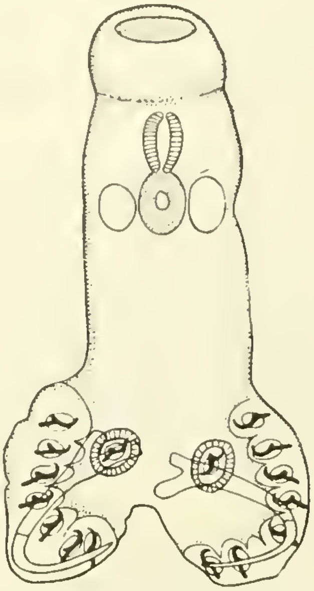

Fig. 218. Sphyranura oligorchis, the subsequent stage of development of the larva. Magnified 215 times. (According to Alvey, 1936).

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[1] Alvey erroneously wrote 0.25 and 0.11 mm; we verified this from his figures.

21. The development of Diclybothrium Leuckart

The genus Diclybothrium is characterized by the presence of the attaching disc with 3 pairs of clamps or suckers, in each of which lies one large chitinous hook. On the posterior end of the disc there is a strongly developed, narrowed part which bears 3 pairs of large hooks (of which two are almost the same size as the hooks of the attaching clamps), one pair of very small hooks and one rudimentary pair of suckers. The typical representative of the genus, D. armatum Leuckart, (Fig. 51), parasitizes the sturgeon family. The study of the development of this species was conducted by us together with A. V. Gussew (Bychowsky and Gussew, 1950). We cite a section of this work relative to the development of D. armatum below.

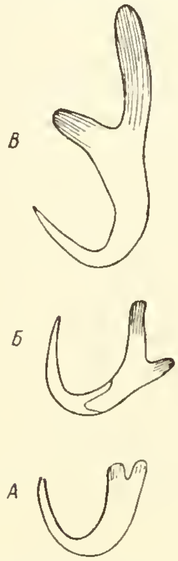

Fig. 219. Sphyranura oligorchis, stages of development of middle hooks, A--On 26th day of development; B--Of the larva which has just emerged from the egg; C--Of an adult worm. Magnified 130 times. (According to Alvey, 1936).

"Attempts to obtain free-swimming larvae of D. armatum were made by us in 1931-1932 but were unsuccessful in the fresh-water region (Delta of the Volga) as in the sea (Island of Sara, Caspian Sea). Only in 1947, during our studies at the VNIRO fish production station in Saratov did we succeed in obtaining two free-swimming larvae from a considerable number of eggs which p. 193 were isolated for development and which, in the main, perished in the early stages of development. A rather large number of the developed larvae could not emerge from the eggs because a rich vegito-bacterial fauna developed on the surface of the latter which prevented the larvae from opening the operculum of the egg. The embryology of the larvae took place in large salt-shakers (stender dishes or embryo dishes? nobis) which were located in a shady place. Temperatures fluctuated strongly during the entire period of development and within a 24-hour period. The temperature during the entire period of the development of the larvae fluctuated from +20.0 to +30.0° centigrade and within the limits of 24 hours the difference was up to 6°. In spite of these clearly unnatural temperature conditions, development took place rather quickly, in comparison with that of other large monogenetic trematodes. On the 6th day lively larvae were already formed in the eggs, and on the 8th day they emerged. Taking into consideration the abnormal conditions of the experiment one must suppose that in nature the development of D.

armatum takes place in approximately 2 weeks. The larva, which has just emerged from the egg ,is torpedo-shaped and is about 0. 4 mm in length when the width of the body is about 0. 18 mm. The attaching disc is clearly delineated from the rest of the body and has a length of 0. 08 mm and a width of about 0. 16 mm. There is a ciliary epithelium distributed in three zones on the surface of the body of the larva. The first zone occupies the surface of the anterior end of the body, extends posteriorly to the level of the pharynx and consists of two sections of ciliary epithelium lying along the edges of the cephalic end and extending somewhat onto the dorsal and ventral surfaces of the body. Both of these sections begin somewhat away from the anterior end so that the extreme anterior end is free of cilia. The second zone begins somewhat above the middle, extends posteriorly almost to the beginning of the attaching disc and is located also in two sections along the sides of the body and also extending somewhat onto the dorsal and ventral surfaces. The third zone is located on the attaching disc,and consists of two lateral sections which begin on the anterior edge of the disc and terminate somewhat just short of its posterior end.

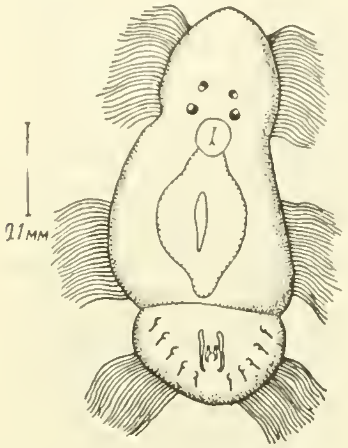

Fig. 220. Diclybothrium armatum Leuckart, free-swimming larva. (According to Bychowsky and Gussew, 1950).

The anterior end of the body bears 2 pairs of rather well-developed eyes located in front of the pharynx. The posterior pair is somewhat larger than the anterior. The pharynx is more or less rounded, about 0. 04 mm in diameter. From it extends the circular intestine of somewhat elongated shape which reaches posteriorly almost to the anterior edge of the attaching disc. The excretory system was not discovered during the studies of both samples. The attaching disc bears a powerful and complex armature consisting of 7 pairs of chitinous hooks of three different types (Fig. 221--B. B.). Among them five pairs are of the same shape and size and are located along the edge of the disc and two pairs differing (from each other, nobis) in shape and sizes and sharply differing from the edge ones lie in the middle section of the disc. The lateral hooks resemble those of the dactylogyrid-type; they have a strongly p. 194
developed hooked part proper and a rather thin, long handle. The interior offshoot of the hooked part is widened in the middle and its sharpened free end is oriented toward the same side as the handle. The sharp points of the lateral hooks are rather strongly curved. Each lateral hook is equipped with a chitinous loop of rather large size customary for all highest monogenetic trematodes. The 1st pair of

middle hooks is much more massive than the lateral ones with a widened and bifurcated upper part. The exterior offshoot of these hooks is somewhat sheered (truncated, nobis) at its free end; whereas its interior is more rounded and massive. The 2nd part of the middle hooks is considerably longer than the first and has a strong point which then sharply curves into a slightly curved handle which has almost a uniform width along its entire length. The length of the lateral hooks is about 0.02 mm and the length of the 1st pair of the middle hooks is about 0.027 - 0.029 mm and that of the second--0.045 - 0.055 mm.

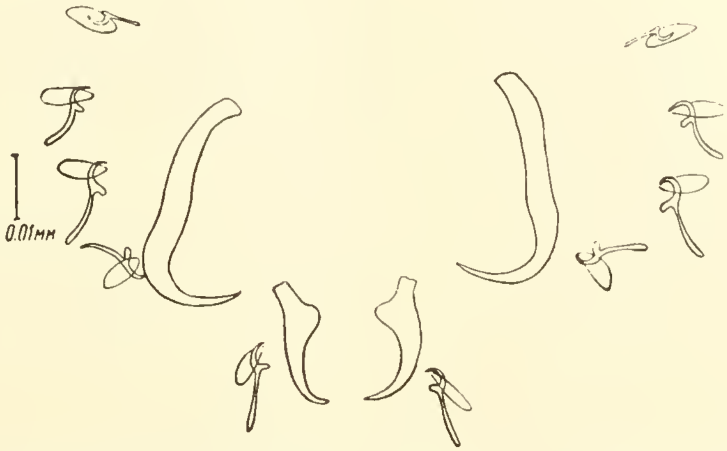

Fig. 221. Diclybothrium armatum Leuckart, attaching armature of the free-swimming larva.

"There is no doubt of the homology of the chitinous hooks of the larva with those of the adult animals. The anterior 3 pairs of lateral hooks correspond to the hooks of the suckers--clamps, the 4th pair to the 3rd pair of hooks of the narrowed part of the disc, the 5th pair corresponds to the small hooks of the posterior end and in such a fashion is the only one of them all not subjected to any noticeable change in sizes or form. The 1st and 2nd pairs of the middle hooks of the larva correspond to those of the narrowed part of the disc of the adult individual. It is curious to note that the lateral hooks, strongly differing in form, and the 2nd pair of middle hooks of the larvae acquire a very considerable similiarity during further development. It is essential to bear this circumstance in mind during the evaluation of the interrelations of the chitinous formations of adult individuals for the formulation of phylogenetic links within the limits of the group."

22. The development of Mazocraes Hermann

Just as all of the subsequent genera, the genus Mazocraes is characterized by the presence of special clamps on the attaching disc which serve for the attachment of the animals. As has been indicated, these clamps have a complex structure because of the presence of a large number of chitinous parts of systematic significance. The genus p. 195 Mazocraes (Fig. 24) is directly diagnosed as Mazocraeidae which have 4 pairs of clamps, 2 large middle hooks and 2 pairs of smaller hooks of different sizes on the attaching disc. The basic difference of this genus from the one closest to it is the special structure of the chitinous parts of the male copulatory organ.

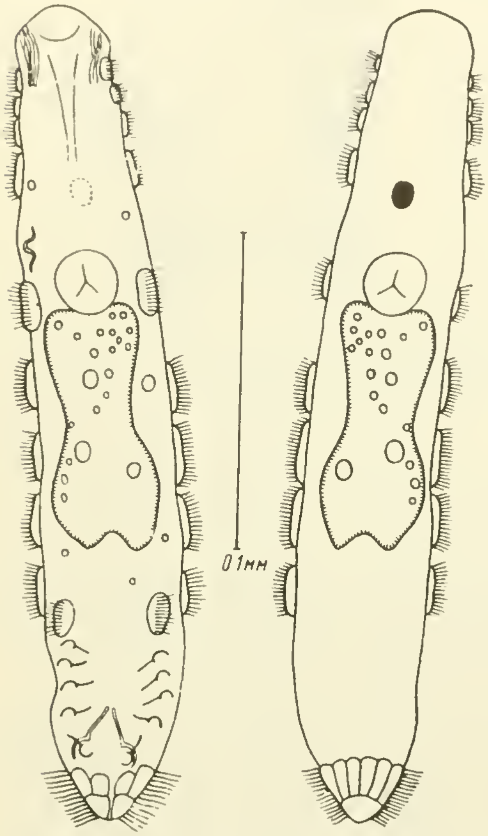

Fig. 222. Mazocraes alosae Hermann free-swimming larva in ventral (on the left) and dorsal (on the right) views.

During our work on the Caspian (Island of Sara, 1932 and 1955) and Black (Sebastapol, 1955) Seas we often obtained early stages of the development of M. alosae Hermann--typical parasite of herring-type fishes. The free-swimming larvae emerge from the eggs on the fourth to the sixth day They are strongly elongated in length, cigar-shaped with a weakly delineated attaching disc. Their length is about 0.2 mm their width is about 0.08 mm. The ciliary covering is distributed along the sides of the body extending onto the dorsal and ventral surfaces. It extends from within a short distance of the anterior end of the body to the anterior edge of the attaching disc and then is located on a cone-shaped growth beyond the disc. The lateral zones of the ciliary epithelium are divided into five cells on each side of the body. Between the cells there are some small but clearly visible sections which are free of ciliary epithelium. The posterior zone is divided into two groups between which lies a relatively large section which forms the rounded apex of the posterior cone which is free of cilia. The anterior end of the larva is slightly rounded and behind it is located a glandular depression slightly divided into two halves. On each side of it (the depression, nobis) and somewhat behind are two pairs of effering ducts of the head glands. Approximately between the first and second

quarters of the length of the body a pigmented eye is located lying mesially from the ventral side of the body. This eye has the shape of a slightly elongated rectangle and apparently is fused from two; the sizes are about 0.001 x 0.005 mm. The eye, well-developed in the larva, disappears rather quickly after the attachment of the latter. The digestive system is represented by a strongly developed pharynx and a sac-like intestine. The pharynx is rounded and is about 0.03 mm in diameter. The intestine, which occupies approximately the third quarter of the length of the body, has a narrowing in the middle part and a small invagination in the middle of the posterior edge forming, in this fashion, 2 posterior lobes. During further development these lobes give rise to two intestinal branches. The p. 196
attaching disc of the larva is equipped with a pair of larger (middle) hooks and 5 pairs of edge hooks (Fig. 223). The large hooks are rather massive with a hard, straight handle and rather powerful point. Their sizes are about 0.028 to about 0.03 mm. The edge hooks have a tender, flexible handle and their terminal little hook is of a different form than among all the preceding species: it is more elongated with a straight edge. The sizes of edge hooks are about 0.2 mm. During further development the chitinous hooks of the larva suffer different fates. The large hooks which lie at the very posterior end of the disc and one pair of edge hooks which is located side by side with them are preserved during the entire life of the animal without any change in shape and sizes. The fate of the second to fifth pairs of edge hooks is completely different. Very soon after the attachment of the larva, the 1st pair of attaching clamps begins to form on the place and foundation of the 2nd pair of edge hooks and then subsequently in the place of the 3rd pair of hooks--the 2nd pair of clamps, etc. until all 4 pairs of clamps characteristic for the adult forms are finally formed. Simultaneously with the beginning of the formation of the 1st pair of clamps on the attaching disc a pair of large middle hooks which have a final form similar to the one in *Dactylogyrus*, with very powerful exterior and somewhat weaker interior offshoots, is incepted and begins to form. Thus the adult form retains 2 pairs of hooks of the larva without any changes and acquires one pair during the postembryonic development. The tempo of development of attaching clamps was not followed through by us; however, we must note their characteristic peculiarity, i. e., their ability to grow. One can

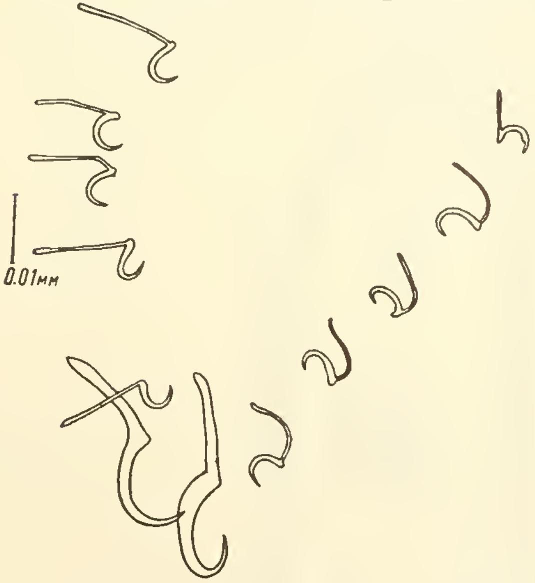

Fig. 223. *Mazocraes alosae* Hermann, attaching armature of the free-swimming larva.

easily see that the younger pairs have considerably smaller sizes on an individual in the process of development which as yet does not have a full number of clamps. The inception of each pair takes place simultaneously, although in rare cases we happened to observe the inception of one clamp somewhat earlier than the other (clamp of the same pair, *nobis*).

23. The development of *Octostoma* Kuhn (=*Kuhnia* Sproston)

During our work in southern Sakhalin in August-September, 1946, we obtained the free-swimming larvae of *O. scombri* Kuhn. Approximately at the same time, the larvae of this species were obtained from European herring by Gallien and Calvez (Gallien and Calvez, 1947). Adult forms of *Octostoma* (Fig. 25) are similar in the structure of the p. 197

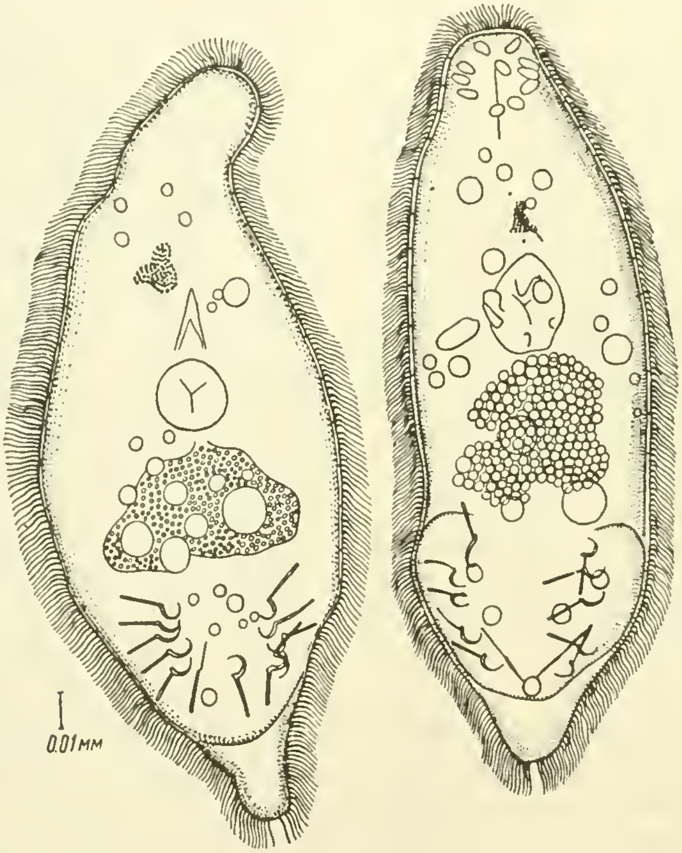

Fig. 224. *Octostoma scombri* Kuhn, free-swimming larva.

attaching apparatus to *Mazocraes*, differing by a somewhat large development of their chitinous parts. According to our data the free-swimming larva (Fig. 224) is spindle-shaped with rounded ends and the greatest width is in the middle of the body. The length of the body of the larva is about 0.23 to 0.26 mm when the width is 0.08 - 0.1 mm. At first the attaching disc is delineated from the body rather weakly but soon unfolds and then extends laterally beyond the general contour of the body. Behind the attaching disc there is a large pyramidal growth which is shed at the same time as the shedding of the ciliary epithelium. The ciliary covering is distributed along the sides of the body extending somewhat to the dorsal and ventral surfaces. The cells of the ciliary epithelium lie in a continuous layer from the anterior to the posterior end including the pyramidal growth. Epithelial cells are flat, elongated and lie with their posterior edges leaning slightly against the following cells. Often one or two of the epithelial cells falls off considerably later than the others and then their borders are even more visible. The anterior end of the larva is equipped with cephalic glands. A large pigmented eye is located between the first and second fourths of the body. This eye does not have p. 198 regular contours and varies from a pyramidal to a tetrahedral shape. Often the pigmented granules of the eye scatter around, so to speak, and the eye gives the impression of degenerating in the larva which has just emerged from the egg. Below the eye is located a rounded pharynx, beyond which lies the metabolizing sac-shaped intestine of irregular shape having microgranular contents of greenish color. The attaching disc bears exactly the same armature (Fig. 225) as among the larvae of Mazocraes alosae Hermann. The sizes of the 5 pairs of edge hooks fluctuate around 0. 02 mm and of the larger pair--about 0. 022 mm. The gradual loss of the ciliary epithelium begins after the attachment of the larva. It starts from the middle of the body and continues progressively to both ends. The posterior pyramidal growth falls off last; at that time the edge hooks unfold and cut through. Further development proceeds just as among Mazocraes alosae. We shall note that the middle hooks which are incepted later reach considerable sizes among adult individuals, and take an active part in attachment.

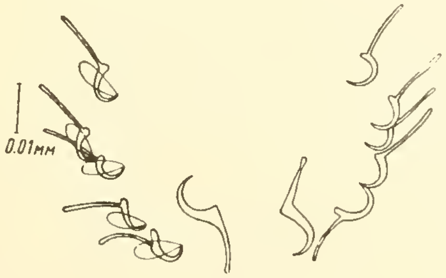

Fig. 225. Octostoma scombri Kuhn, attaching armature of the free-swimming larva.

The data of Gallien and Calvez basically coincide with ours; however, the only difference is that they did not notice the differences in sizes of the chitinous hooks which, it is true, are very insignificant.

24. The development of Diclidophora Diesing (=Dactycotyle Beneden and Hesse, Dactylocotyle Marshall)

The genus Diclidophora (Fig. 54) represents a large group of marine monogenetic trematodes which are characterized by the presence of 8 sucker-shaped clamps on the disc and by a system of chitinous plates which, in contrast to the plates of Mazocraeidae, are strongly dismembered and serve mainly as the supporting apparatus of the suckers. The three species of this genus for which larvae are known are: *D. luscae* (Beneden and Hesse), *D. pollachii* (Beneden and Hesse), and *D. denticulata* (Olsson). The larvae of the first two species were studied by Gallien (Gallien, 1934a), but it is we who obtained the last one from the eggs which were brought to us alive by A. V. Gussew and U. I. Polianski from the Norwegian Sea. The eggs of *D. denticulata* were gathered by them from parasites from the gills of the Pollack--Pollachius virens (L.).

Upon emergence from the eggs the larva of *Diclidophora* (Fig. 226) swim freely with the help of the ciliary epithelium which is located just as it is among the *Mazocraes* with a break at the level of

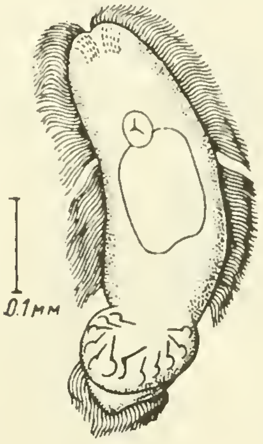

Fig. 226. *Diclidophora denticulata* (Olsson), free-swimming larva.

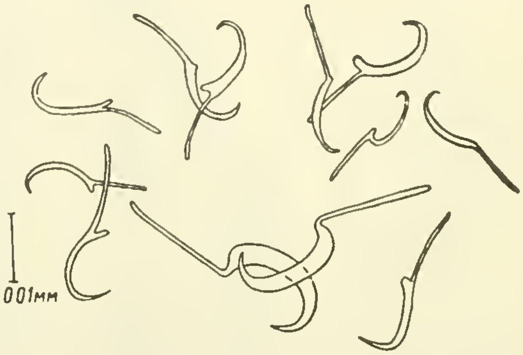

Fig. 227. *Diclidophora denticulata* (Olsson), attaching armature of the free-swimming larva.

attaching disc. The dorsoventrally flattened larvae are transparent. The length of the larvae of *D. luscae* (Beneden and Hesse) in average contraction is 0.195 mm, its width is 0.08 mm. The sizes of the larva of *D. pollachii* (Beneden and Hesse) are not indicated by Gallien, just as the other data, as a matter of fact, for he writes only about this larva that it completely similar to *D. luscae* (Beneden and Hesse). The length of the larva of D. denticulata (Olsson) is about 0.35 mm whereas the width is 0.15 mm. At the level of the beginning of the posterior quarter p. 199
of the body of the larva, the attaching disc begins, which occupies in length one-half of this quarter; the second half forms a powerful cone-shaped growth. The larvae of all species are devoid of eyes. Their pharynx is rounded and extends into a strongly developed sac-like intestine which sometimes extends posteriorly into the attaching disc. The excretory and other systems of organs were not discovered. The attaching armature consists of 12 hooks of the same type as among *Mazocraes* (Fig. 227); 10 edge hooks of approximately the same length and 2 larger

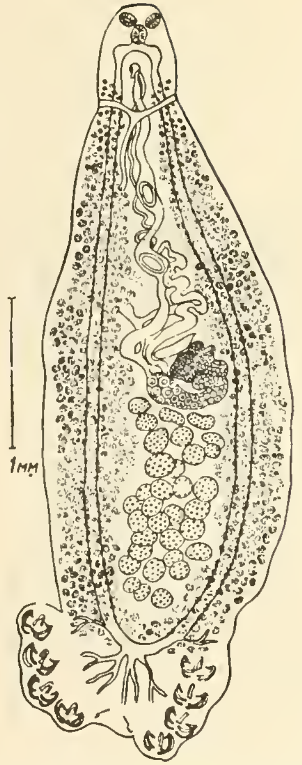

Fig. 228. Discocotyle sagittata (Leuckart), adult worm from the gills of Coregonus lavaretus (L.) from Lake Ladogskoe.

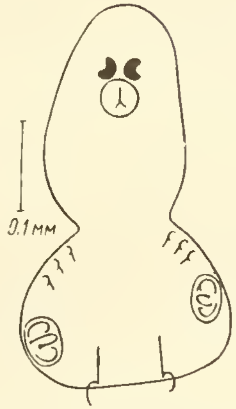

Fig. 229. Discocotyle sagitta (Leuckart), dead larva with unfolded disc which has lost its ciliary epithelium.

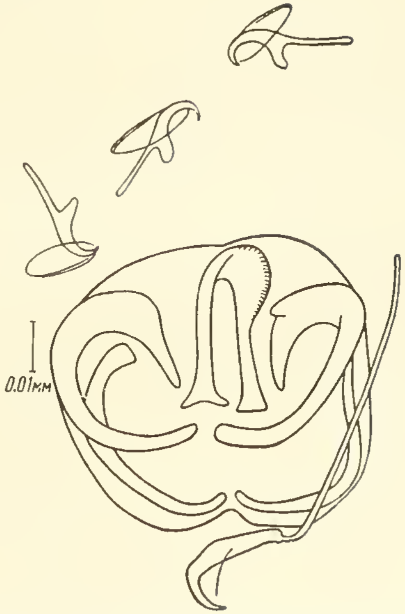

Fig. 230. Discocotyle sagitta (Leuckart), attachment armature (right half) of the free-swimming larva.

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middle hooks. Gallien indicates that for D. luscae the 3rd pair is the largest; we did not observe this in D. denticulata. The sizes of the edge hooks in D. luscae are about 0.025 mm and among D. denticulatus somewhat smaller--0.02 - 0.023 mm. The middle hooks have a somewhat different shape than the edge hooks: the transversal offshoot is absent at the place of transition of the terminal hook into the handle. The length of the middle hooks of the larvae of D. luscae is 0.028 mm and of D. denticulata--0.03 mm.

25. The development of Discocotyle Diesing

The genus Discocotyle (Fig. 228) is distinguished from the closest species by the peculiarities of the structure of the sex system, particularly by the absence of the sex sucker and by the presence of vaginal ducts and follicular testes. Four pairs of clamps of the same size and of the usual type are characteristic for it. We obtained larvae of D. sagittata (Leuckart) from individuals taken from the gills of the Whitefish, Coregonus lavaretus (L.) from the live fish bank (aquarium, nobis) in Leningrad (in October 1951). The free-swimming larva emerged on the 19th day after the deposition of eggs. Unfortunately the larvae came out at night and we could only observe them after they had lost the ciliary epithelium. The larvae (Fig. 229) at our disposal already had an unfolded and relatively very large disc and a body flattened dorsoventrally. The sizes of the larva: general length about 0.42 mm, the width of the body 0.16 mm; the sizes of the disc 0.15 x 0.23 mm. The larva is equipped with 2 pigmented eyes located directly above the rounded pharynx. We did not succeed in examining the internal organization of the larva. The attaching disc of the larva is equipped with 2 p. 201 large hooks and 3 pairs of edge hooks and one pair of well-developed attaching clamps (Fig. 230). The large pair of the hooks have a sickle-shaped curved basic part with a rather powerful point. A very long thin handle emerges from the interior edge of its upper end. The length of the entire hook is 0.082 mm and of the handle 0.06 mm. In contrast to the middle hooks of the dactylogyrid-type these hooks bend easily at the place of the junction of the handle and the basic part, besides that the handle itself is very resilient and can easily bend. The edge hooks are of the usual type with a strongly developed point; their length is about 0.025 mm. The clamps of the larva have the same structure as in the adult. Their sizes are 0.06 x 0.008 mm; thus if we take into consideration that among the adult individuals the first pair of clamps has the size of 0.2 mm x 0.28 mm we see that in spite of their constant shape the clamps of the larva are many times smaller, consequently they grow powerfully. Data on further development are absent but the general process of the development of the chitinous armature of the disc is clear. It is interesting to note that among adult individuals the eyes are absent, having been reduced during the time of development.

26. The development of *Diplozoon* Nordmann

The development of the common parasite of carp fishes, *D. paradoxum* Nordmann(Fig. 231) was studied by Zeller (Zeller, 1872b) and by us; however, one must indicate that the existing data concerning the structure of the larva are insufficient and need to be supplemented. According to our data, the larvae emerge from the eggs on the 9th to the 10th day and according to Zeller on the 12th - 17th. The free-swimming larva (Fig. 232) has an elongated form with a small band at the level of the anterior end of the pharynx with a weakly expressed attaching disc and a cap-shaped growth behind the latter. According to Zeller, the length of the larva is about 0.26 p. 202 mm and, according to our data, about 0.23 mm. The ciliary covering of the larva is strongly developed and is represented by five groups of cells. The first two groups lie along the sides of the anterior part of the body somewhat away from the anterior end and reach back to the above-mentioned band. The two next groups also occupy the sides of the body starting a little below the band and reach posteriorly to the level of the anterior edge of the attaching disc. Finally, the fifth group lies beyond the disc on the posterior growth of the body. Two small buccal suckers are located on the cephalic end somewhat lower than the buccal opening; a little below them are located 2 bean-shaped, pigmented eyes drawn close together so that their convex sides touch or even merge. The digestive system of the larva is strongly developed. The above-mentioned suckers, which are characteristic for the entire group of Oligonchoinea, are located on each

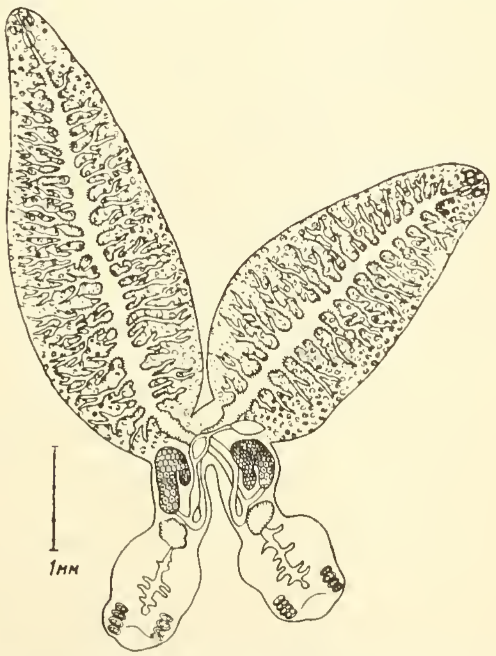

Fig. 231. *Diplozoon paradoxum* Nordmann, pair of adult worms from the gills of *Abramis brama* from the Bay of Finland near Peterhof.

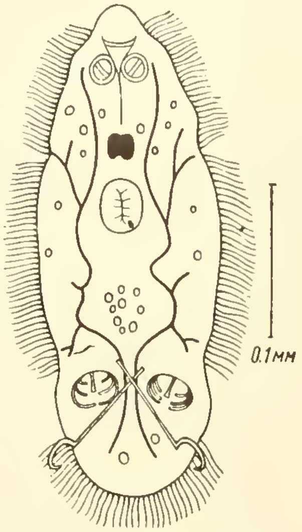

Fig. 232. *Diplozoon paradoxum* Nordmann, free-swimming larva.

of the sides of the funnel-shaped buccal cavity, which is almost at the very anterior end of the body. The pharynx is somewhat elongated (0.035 x 0.032 mm) and lies behind the eyes. A long pipe-shaped intestine which forms small lateral outgrowths is located behind the pharynx. The excretory system is poorly visible. Its openings are located laterally at the place of the break between the first two ciliary zones and the following ones. The excretory trunks extend posteriorly, curving in and out symmetrically along both sides of the body and enter, branching off,into the attaching disc. Two smaller trunks ,which extend forward along the sides of the pharynx and extend above to the level of the buccal suckers emerge from the two basic excretory trunks. The attaching disc bears a pair of large hooks and 2 attaching clamps of the usual form and structure (Fig. 233). The sizes of the clamps are about 0.04 x 0.05 mm. The hooks are of the same shape as among Discocotyle sagittata (Leuckart). They are divided into the end hooks, strongly elongated and having a weakly curved point, and into a thin bending handle which is about 2 to 2 1/2 times longer than the end hook. The general length of the hooks is 0.07 to 0.11 mm. We can observe in live larvae that the points of these hooks protrude outside from the very moment of the emergence of the larva from the egg. They move very actively, not only during the moments of the settling of the larva, but also during its swimming. The edge hooks were neither discovered by Zeller nor by us and it can be considered almost certain that they are absent. This circumstance cannot cause special astonishment because D. paradoxum represents a very specialized and isolated species. After the attachment of the larva (diporpa) to the gills of its host it loses the ciliary epithelium, begins to feed and undergoes further changes. At this time a small sucker is formed on the ventral side of the body, somewhat closer to the posterior than anterior end, p. 203
while on the dorsal side correspondingly but still closer to the posterior end of the body a small growth (Fig. 234 A) is also formed. At the same time the other pairs of attaching clamps begin to be incepted in sequence. Mostly around the moment of the inception of the second pair of clamps, the larvae meet in pairs and unite, continuing further development together (Fig. 234 B). Often, however, one can observe that the junction

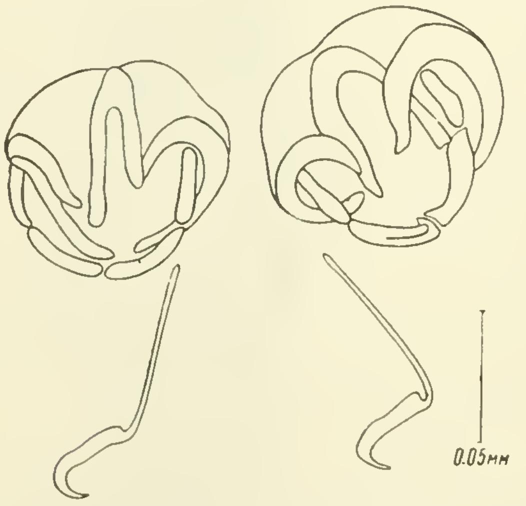

Fig. 233. Diplozoon paradoxum Nordmann, attaching armature of the free-swimming larva (somewhat flattened).

of the larvae takes place later when they already have a developing or already developed 3rd pair of clamps. Also,one can often observe the non-simultaneous development of clamps so that on one side of the disc there are 3,and on the other,2 clamps (Fig. 234 C). Finally, we happened to observe the union of larvae which are in different stages of development of the attaching apparatus, i.e., having different ages. The individuals which were united in one or the other fashion gradually grow together and at the same time their attaching clamps gradually acquire the final number and sizes. The pigmented eyes disappear during the early stages of development; for the most part this takes place approximately at the appearance of the ventral sucker.

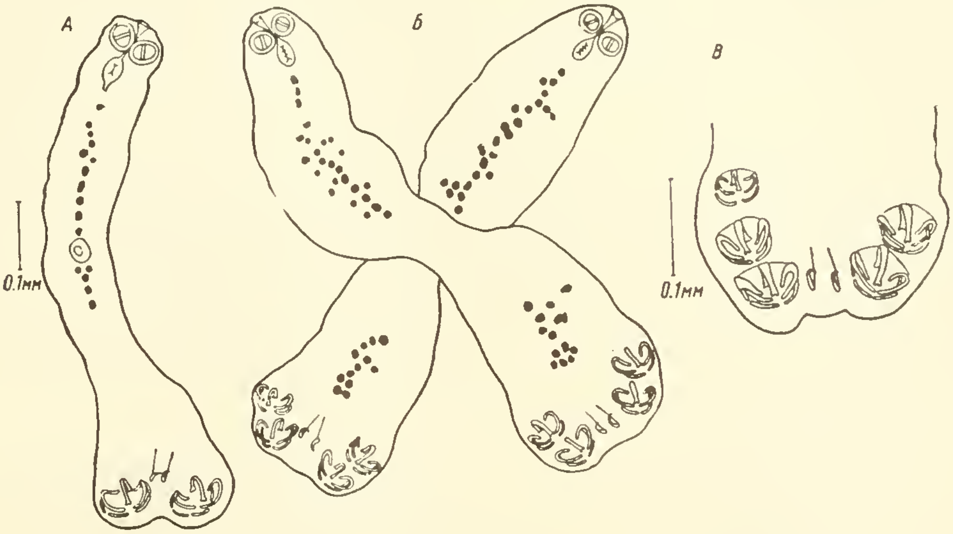

Fig. 234. Diplozoon paradoxum Nordmann, stages of development of the worms from the gills of Abramis brama from the Bay of Finland near Peterhof. Explanation in text.

The development of the sex system and the process of the merging of the larva has not been studied in detail, just as the development of the excretory system, which is powerfully developed among adult worms, has also not been studied. One must note that certain differences between the data of Zeller and ours (which have not been especially mentioned here) probably are due to the fact that our data relate to D. paradoxum which was collected from the Bream (Abramis brama L.), whereas the data of Zeller are from parasites of the Minnow (Phoxinus phoxinus L.). In the materials of A. V. Gussew there are data on D. paradoxum and its development from the Island of Hanka from the gills of Erythoculter mongolicus Basilewsky; basically these data coincide with ours.

27. The development of Microcotyle Beneden and Hesse

The genus Microcotyle is characterized by a powerful development of the attaching disc on which is located a considerable number of pairs of attaching clamps of the same shape ,lying more or less symmetrically in relation to the long axis of the disc. Altogether, 6 species of Microcotyle have been studied with varying degrees of completeness, of which three were studied by us, one by our collaborator, U. A. Strelkov, one by Remley (Remley, 1936, 1942) and finally one by Sproston (Sproston, 1946). Because of the fact that the genus Microcotyle undoubtedly is very artificial and during subsequent works will probably be subdivided into a number of smaller genera, we considered it more convenient to express the existing data on each species separately, beginning with the data of Remley.

Microcotyle spinicirrus MacCallum--is a parasite of the North American fresh-water fish, Aplodinotus grunniens Raf. (Fam. Sciaenidae), the development of which was studied by Remley. Adult worms (Fig. 235), which reach up to 13 mm in length, are distinguished by a powerful development of the attaching disc which is located completely behind the body so that the last testes lie anterior to its bebinning. The number of attaching clamps is very large, up to 50 on each side. The free-swimming larva which has just emerged from the egg of M. spinicirrus is 0. 23 mm in length and 0. 1 mm in width (Fig. 236). It is flattened dorsoventrally and has a more or less oval form. The ciliary covering is represented by three zones of ciliary epithelium along the

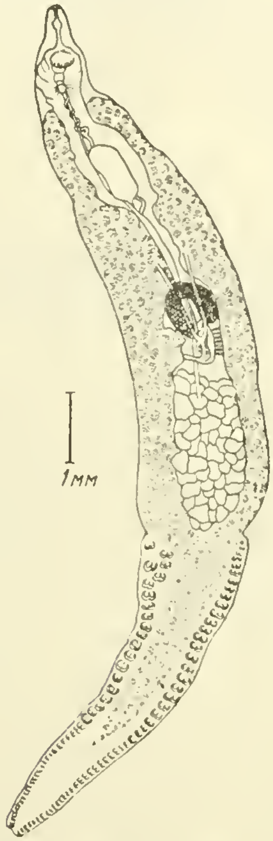

Fig. 235. Microcotyle spinicirrus MacCallum, adult worm. (According to Remley, 1942).

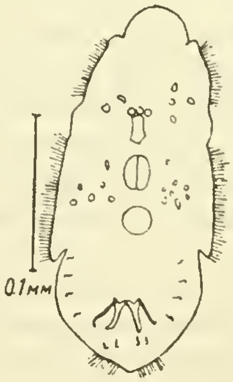

Fig. 236. Microcotyle spinicirrus MacCallum, free-swimming larva. (According to Remley, 1942).

sides of the body. The first zone begins somewhat away from the anterior end of the body and reaches the level of the anterior end of the pigmented p. 205 eye. The second zone extends from the posterior end of the eye to the attaching disc, and the third lies on the posterior edge of the disc (judging by the drawing of Remley--on a cone-shaped growth). The author did not observe the suckers of the buccal cavity in the larvae. There is a slightly elongated pharynx located on the border between the anterior and posterior halves of the body. It opens posteriorly into the sac-like, rounded intestine. A pigmented little eye of almost rectangular form (0.018 x 0.01 mm) lies between the pharynx and the anterior end of the body. The excretory system has not been studied; there are 3 pairs of flame cells (?--B. B.) one of which is located in front and to the side of the eye with the second along the sides of the anterior end of the pharynx, whereas the third is on the sides of the body behind the intestine. The attaching disc occupies the posterior one-third of the entire body. It is equipped with 12 edge hooks along the edges and 2 pairs of large hooks in the middle of the disc (Fig. 237). The edge hooks are of the same form as among Mazocraes, about

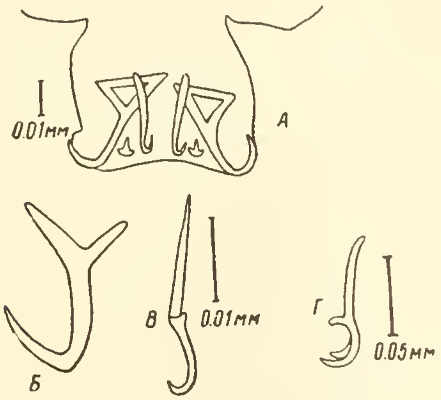

Fig. 237. Microcotyle spinicirrus MacCallum, attaching armature of the posterior end of the disc of the young worm (before the loss of the cercomere). A--Cercomere; B, C--large middle hooks; D--edge hooks. (According to Remley, 1942).

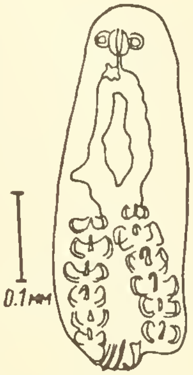

Fig. 238. Microcotyle spinicirrus MacCallum, young worm with six pairs of clamps and the "cercomere" (according to Remley, 1942).

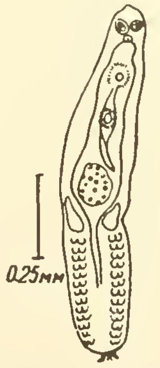

Fig. 239. Microcotyle spinicirrus MacCallum, young worm with 13 pairs of clamps and with a "cercomere", (According to Remley, 1942).

0.08 mm in length. The 1st pair of middle hooks has a weakly curved point and straight base, between which there is a small widening. This pair more closely resembles somewhat-altered edge hooks in its structure than middle hooks. The 2nd pair has a typical dactylogyrid shape with a powerful point and well-developed extensions. The length of the 1st pair is about 0.024 mm and the 2nd about 0.022 mm. Further development has been poorly studied. The youngest individuals discovered on the host (Fig. 238) already have 6 pairs of formed attaching clamps and a small growth in which are located one pair of lateral hooks, and 2 pairs of middle hooks remain on the posterior end of the disc. The sex system begins to be incepted but the sex armature has not yet been formed. Suckers of the buccal cavity are incepted on the anterior end of the body along the sides of the pharynx. During further development a gradual increase in the number of pairs of attaching clamps takes place until it reaches the final size. The development of the interior organs takes place simultaneously with this. The outgrowth which bears the edge and middle hooks (of the "larval" attaching disc according to Remley) is preserved until the development of 13 pairs of attaching clamps (Fig. 239), but among the majority which have from 10 to 15 pairs it is absent, just as among all older individuals. The sex armature is incepted approximately toward the time of the disappearance of the "larval" attaching disc or somewhat later. The testes are incepted earlier than the ovary. p. 206

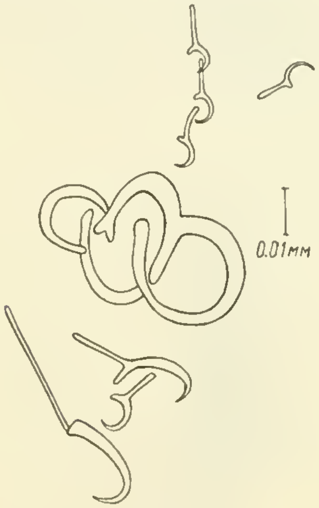

Fig. 240. *Microcotyle mugilis* Vogt, attaching armature (left half) of the larva which was extracted from the egg.

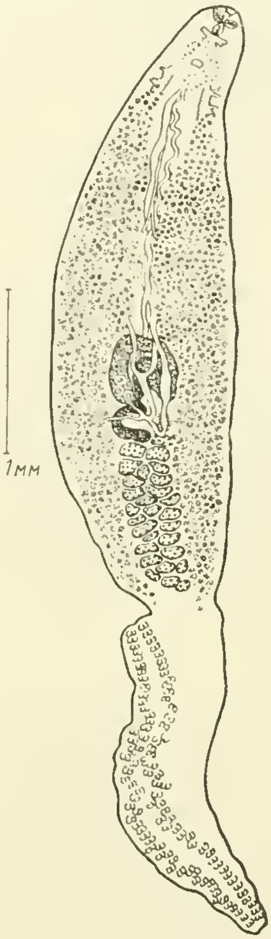

Fig. 241. *Microcotyle pomatomi* Goto, adult worm from the gills of *Pomatomus saltatrix* (L.) from the region of Sebastopol (Black Sea).

The process of formation of sex ducts has been poorly studied. The appended figures give certain notions about it (Figs. 238, 239).

Microcotyle mugilis Vogt (Fig. 23)--It is a common parasite of Black Sea gray mullets (*Mugis* sp. sp.) and is characterized, just as the preceding species, by the disc,located behind the body but its number of clamps is considerably smaller--up to 30 on each side. We obtained the development of this worm at the Sebastopol Biological Station in 1935, but unfortunately the larvae which had already been formed and which moved vigorously inside the eggs could not emerge and perished because of a powerful growth of microscopic weeds and bacteria around the egg. We took them out of the eggs in somewhat damaged condition and because of that we cannot give detailed information about the sizes of the larvae and their ciliary covering. The larva has a well-developed pigmented eye, a rounded pharynx and a sac-shaped intestine. The attaching disc (Fig. 240) is equipped with 10 edge hooks, 2 pairs of middle hooks, p. 207
and one pair of attaching clamps. If one takes into consideration therefore, that these clamps are incepted at the place of the edge hooks during their transformation the nature of the armature corresponds to that of *M. spinicirrus* Remley. The structure of the edge hooks is the same as among this type while the middle hooks have a somewhat different structure. The first pair of middle hooks strongly resemble the large middle hooks of *Discocotyle* and *Diplozoon* in shape. They consist of two parts: a hook with the base widened at the top and with a rather strong point and of a thin, long chitinous little stick which joins with the interior angle of the upper part of the base. The 2nd pair has powerful hook parts and a more weakly developed handle. The transversal offshoot between them is developed rather strongly which makes their shape resemble the edge hooks . On the other hand these hooks, as is evident from *M. spinicirrus* Remley, can be likened to the usual ones and then (one may, *nobis*) speak about a more powerfully developed extension of the middle hooks. The pair of attaching clamps is developed very distinctly and already has all the same chitinous parts as the clamps of the other individuals. The sizes of the edge hooks are about 0.014 - 0.016 mm, of the 1st pair of middle hooks--0.05, of the 2nd pair--0.03 mm; the attaching clamps are 0.025 mm with a width of 0.04 mm. We did not obtain any stages intermediate between the mature individuals and the free-swimming larva.

Microcotyle pomatomi Goto (Fig. 241)--A parasite of Black Sea Bluefish -- *Pomatomus saltatrix* (L.), has a structure resembling the two preceding species but with a more powerful attaching disc on which lie from 90 to 100 pairs of clamps than among *M. spinicirrus* Remley. In contrast to the preceding species this *Microcotyle* has numerous chitinous thorns in the sex cloaca and not a crown of large thorns on the copulatory organ. During his work at the Sebastopol

Biological Station in August 1950, U. A. Strelkov obtained the free-swimming larvae. The larvae (Fig. 242) emerge from the eggs 4 days

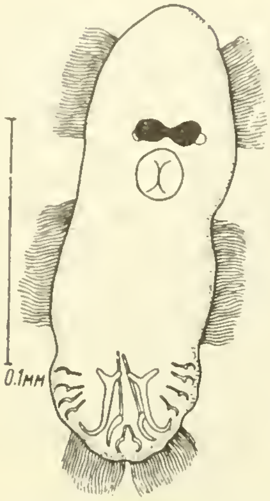

Fig. 242. Microcotyle pomatomi Goto, free-swimming larva.

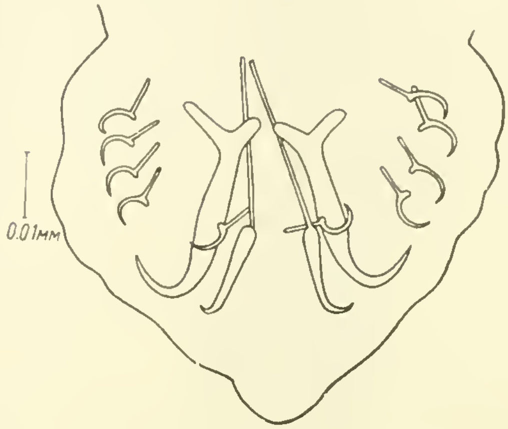

Fig. 243. Microcotyle pomatomi, Goto, attaching armature of the free-swimming larva.

after deposition of the egg. They have an elongated torpedo-shaped p. 208 form, 0.2 mm in length and 0.06 mm in width. The ciliary covering is located in three zones just as in M. spinicirrus. The distribution of the zones is the same: the last, somewhat more powerful zone lies on a cone-shaped growth and is divided by its tip into two halves. It has a well-developed pigmented eye. One specimen at our disposal had two eyes developed to absolutely the same degree; nowhere have we ever observed such a monstrosity. The entire structure of the larva cannot be determined from the preparations. The attaching disc is fairly well-delineated from the body, it bears 5 pairs of edge and 2 pairs of middle hooks (Fig. 243). The edge hooks are distributed just as among the preceding types, i.e., one pair between the middle hooks and the rest somewhat higher along the sides of the disc. The 1st pair of the middle hooks is of the same shape as among M. mugilis, but is somewhat more massive. Even though it does resemble that of M. spinicirrus Remley in type or M. mugilis Vogt the 2nd pair is, nevertheless, considerably different. The hooks of this pair resemble the middle hooks of the lowest monogenetic trematodes. They have a basic part elongated and widened in the middle, they have strongly curved powerful point and small offshoots--extensions, standing at almost right angles to each other. The length of the edge hooks is about 0.012 mm, the length of the 1st pair of middle hooks is 0.042 mm and of the 2nd pair--0.026 mm. In the material collected by U. S. Strelkov there are no stages of development subsequent to the larva.

p. 209

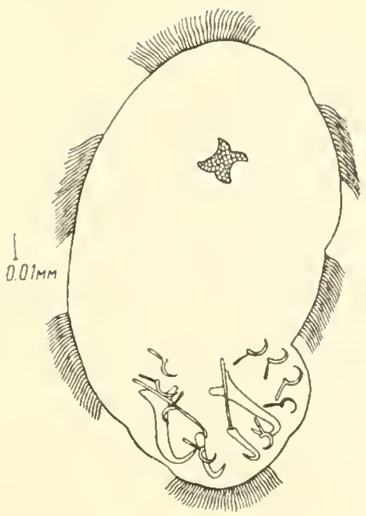

Fig. 245. Microcotyle sebastis Goto, free-swimming larva.

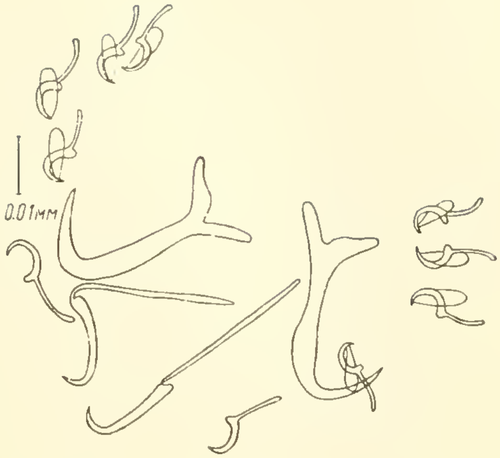

Fig. 246. Microcotyle sebastis Goto, attaching armature of the free-swimming larva.

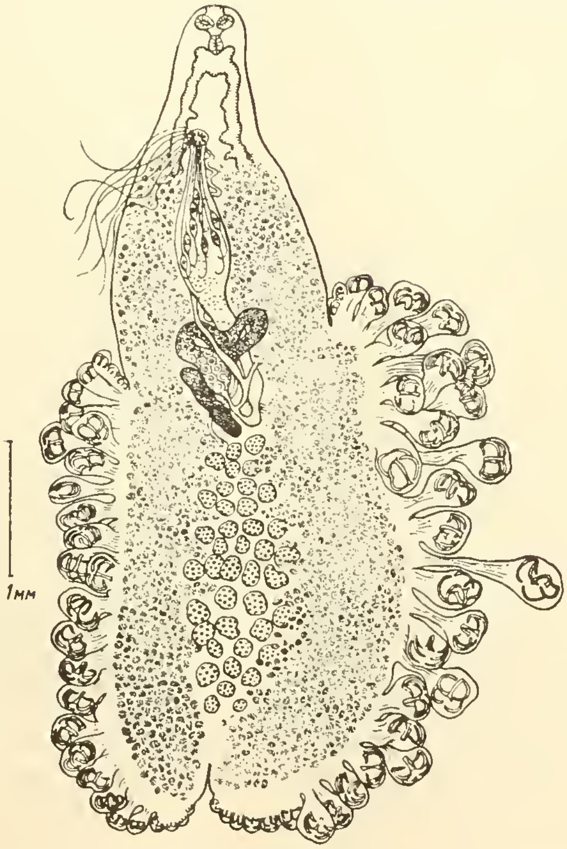

Fig. 247. Microcotyle gotoi Yamaguti, adult worm from the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

Microcotyle sebastis Goto--Parasitizes the gills of Sebastodes schlegelii (Hilgend.). Just as among M. pomatomi Goto, the adult worms of this species (Fig. 244), are distinguished by the powerful development of the disc, but in contrast to the latter species, bear only 25 to 30 clamps. Similarly the sex atrium of M. sebastis is equipped with numerous little thorns but of different shape and greater number than among M. pomatomi. We obtained free-swimming larvae of this species in July 1949 in Vladivostok. They emerge from the eggs on the 10th to the 11th day after deposition of the latter. They have an elongated, cigar-shaped body (Fig. 245) with a well-developed attaching disc. The length of the larva is 0.018 to 0.022 mm, with a width of about 0.05 mm. The ciliary covering of the larva is strongly developed so that during the observations of live subjects its seems that it covers all the edges of the body. Actually, however, the ciliary epithelium is distributed into three zones just as it is among M. pomatomi. The interior organization of the larva has not been studied by us. There is a well-developed pigmented eye lying at the end of the first third of the body. The attaching armature of the larva consists of 2 pairs of middle and 5 pairs of edge hooks (Fig. 246). The edge hooks and the 2nd pair of middle hooks have absolutely the same structure as in M. pomatomi. The 1st pair of middle hooks resembles that of M. pomatomi but is considerably thinner and straighter. The length of edge hooks is 0.013 - 0.016 mm; p. 210
of the 1st pair of middle hooks is 0.042 - 0.045 and 2nd pair 0.026 - 0.029 mm. We did not succeed in observing the subsequent stages of the development of this species.

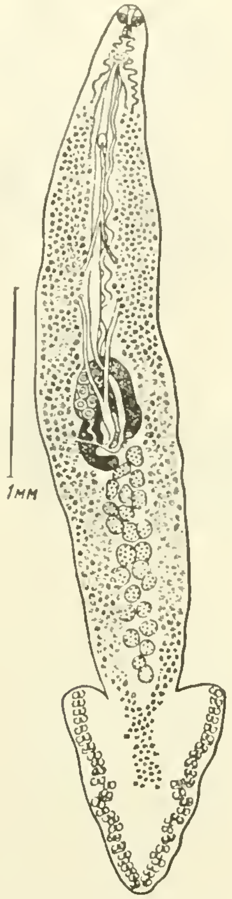

Fig. 244. Microcotyle sebastis Goto, adult worms from the gills of Sebastodes shlegeli (Hilgend.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

Microcotyle gotoi Yamaguti--is encountered very often on the gills of Terpugs--Hexagrammos octogrammus (Pal.). In contrast to all preceding ones, this species has a disc which extends considerably forward along the sides of the body so that the ovary and the testes lie behind the upper edge of the disc and of the clamps located on it (Fig. 247).

During the work on southern Sakhalin (1946) and the Island of Shikotan (1949) we studied the development of M. gotoi, starting from the early stages of the attached larva until its attainment of maturity. Unfortunately we did not succeed in obtaining a free-swimming larva of this species because the eggs, which were isolated in special containers, perished during the early stages of development. The earliest stage of development of M. gotoi (Fig. 248) which was discovered on the gills of Terpug, is close to the free-swimming larva of M. sebastis. The general length of the body of the larvae is about 0.3 mm and 0.11 mm in width. It is devoid of ciliary epithelium and has an elongated shape and the disc is somewhat wider than the body proper. On the anterior end there are 2 fully developed buccal suckers lying next to each other, somewhat above the rounded pharynx. The intestine is clearly visible, it is filled with partially digested food (remnants of the pigment of the haemoglobin of the blood of the host), is sac-shaped, elongated (and extends, nobis) up to the beginning of the disc. The pigmented eye is absent although it probably exists in the free-swimming larva. The attaching armature consists of 2 pairs of middle hooks and 5 pairs of edge hooks (Fig. 249). The edge hooks have the usual shape for the genus, lying in three groups: 4 hooks along the edge of the disc on each side and above both pairs of the middle hooks and the remaining 2 between the middle ones near the lower edge of the disc. The 1st pair p. 211
of middle hooks resembles those of M. spinicirrus Remley but, as is apparent from the drawing, one of them is considerably coarser and more

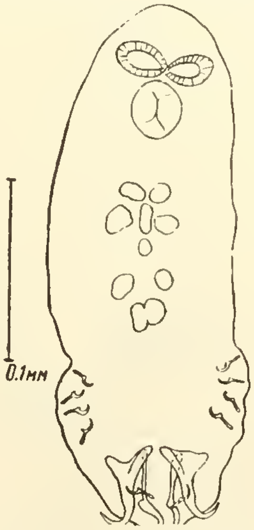

Fig. 248. Microcotyle gotoi Yamaguti, larva which has recently attached to the gills of Hexogrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

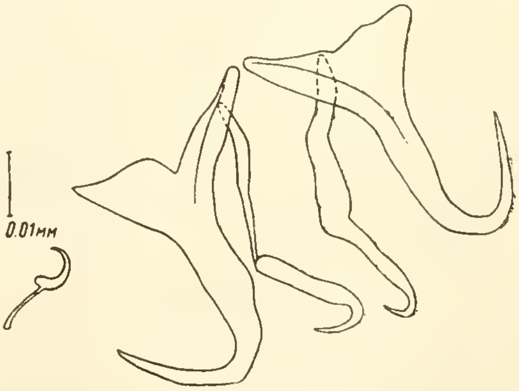

Fig. 249. Microcotyle gotoi Yamaguti, middle and one edge hook of the larva which recently attached itself to the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

massive than the other. Both hooks resemble the developing hooks of the dactylogyrid-type with a fully developed basal part and undeveloped extensions. In one of them the upper edge is truncated, almost straight and somewhat thinned in the middle, whereas the anterior edge is considerably thickened. The second hook gives the impression of being somewhat more developed, in it two extensions are noticeable, so to speak. The 2nd pair of hooks also is not altogether similar to those of *M. spinicirrus*, the middle hooks lie on the posterior end of the disc and the first pair is closer to its longitudinal axis. The sizes of the middle hooks of this larva are 0.016 mm, and the 1st pair of the middle hooks--0.045 mm, and the 2nd--0.051 mm. The subsequent stages of development resemble the free-swimming larva of *M. mugilis* Vogt. Its average length is about 0.35 mm with a width of 0.1 mm. The larva has an elongated form (Fig. 250) with a well-developed attaching disc located in such a way that the ends of its middle part strongly extend beyond the general contour of the body and contain in them more-or-less developed clamps, on.on each side. These lateral growths lie in a different plane (closer to the back) than the remaining part of the disc. The disc extends beyond the growths in the shape of a rather long very mobile offshoot and in normal conditions is almost rectangular or square shaped (about 0.06 x 0.05 mm). Just as in all the subsequent stages of development the larva does not have a pigmented eye. Three groups of efferent ducts of the head glands open at the anterior end. There are two well-developed suckers of the buccal

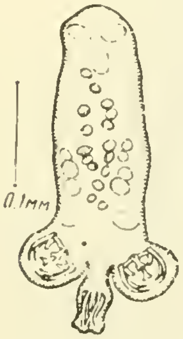

Fig. 250. *Microcotyle gotoi* Yamaguti, larva with one pair of clamps and one offshoot from the gills of *Hexagrammos octogrammus* (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

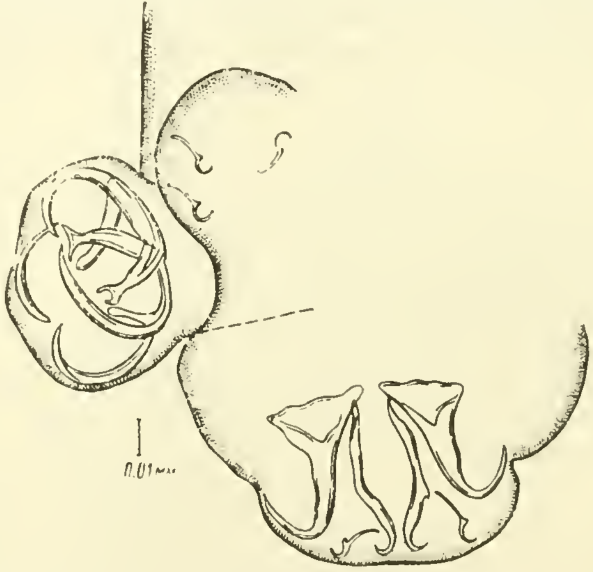

Fig. 251. *Microcotyle gotoi* Yamaguti, part of the attaching disc of the larva with one pair of clamps and one posterior offshoot from the gills of *Hexagrammos octogrammus* (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

funnel with clearly expressed transversal septa. The pharynx is rounded, about 0.04 mm in size and leads into a well-developed, sac-shaped intestine. The armature of the attaching disc has already changed (Fig. p. 212 251). There are 2 pairs of middle hooks, 4 pairs of edge hooks, and attaching clamps are formed instead of the 5th pair. The remaining edge hooks lie in such a fashion that the developing clamps locate between the 3 upper pairs and the complex of the middle hooks and the 2 remaining edge hooks. The sizes of the edge hooks of this stage are 0.017 - 0.019 mm, of the 1st pair of middle hooks--0.05 mm, of the second--0.052 mm, and the attaching clamps 0.06 x 0.035 mm. Subsequent development takes place rather quickly. Just as among the Mazocraes and other close forms, subsequent pairs begin to be incepted at the place and from the edge hooks which lie in front of the 1st pair of the attaching clamps until the stage of the 4 pairs of clamps has been reached and then the following pairs are incepted completely anew until 33 - 35 pairs, which are characteristic for the adult individuals, are reached. The inception of each pair takes place mainly simultaneously, although one often observed faster development of clamps on one side. Thus, one often observes individuals with 5-6 clamps on one side and 6-7 on the other (Fig. 252).

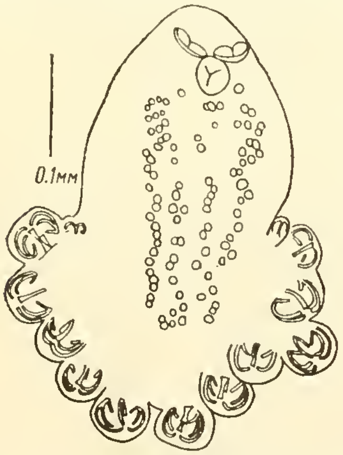

Fig. 252. Microcotyle gotoi Yamaguti, young worm with 6 clamps on one side of the disc and 7 on the other from the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

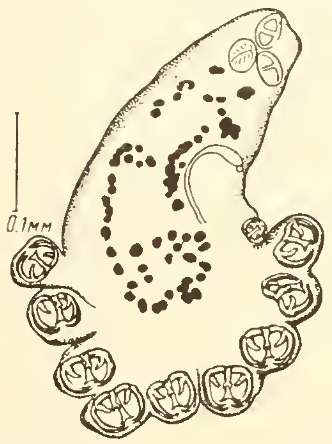

Fig. 253. Microcotyle gotoi Yamaguti, young worm with 5 clamps of which the left fifth clamp is more weakly developed than the right one from the gills of Hexagrammus octogrammus (Pal.) from the region of Yablichnoii (southern Skahalin, Sea of Japan).

Along with this one must note that the clamps are incepted considerably smaller than among adult animals; this has already been indicated earlier (see page 196). However, one can often observe that on one side, the last of the clamps which was formed is still of small size, whereas the corresponding one on the other side has already reached or almost reached its final size (Fig. 253). The posterior outgrowth of the attaching disc, containing in it 2 pairs of middle hooks and one pair of edge hooks which do not change, is preserved until the time of formation

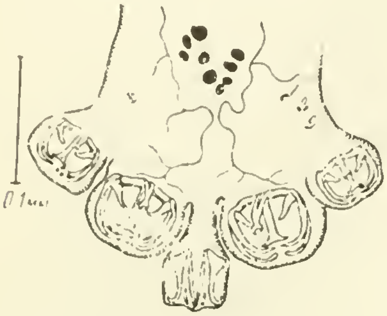

Fig. 254. Microcotyle gotoi Yamaguti, a larva with two pairs of clamps in the cercomere from the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

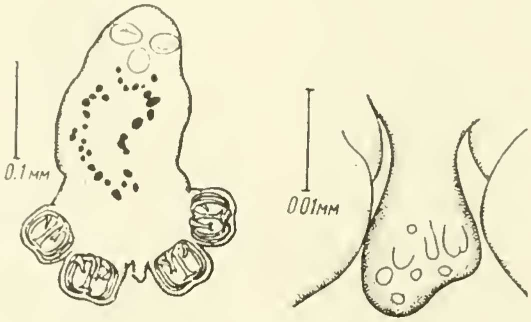

Fig. 255. Microcotyle gotoi Yamaguti, young worms with two pairs of clamps and the drop-shaped remnant of a cercomere with a vacuolized posterior end from the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

of the 2 pairs of attaching clamps. At that time its parenchyma is strongly vacuolated and this part of the disc (cercomere!) falls off (Fig. 254). Immediately following this a small, drop-shaped growth p. 213

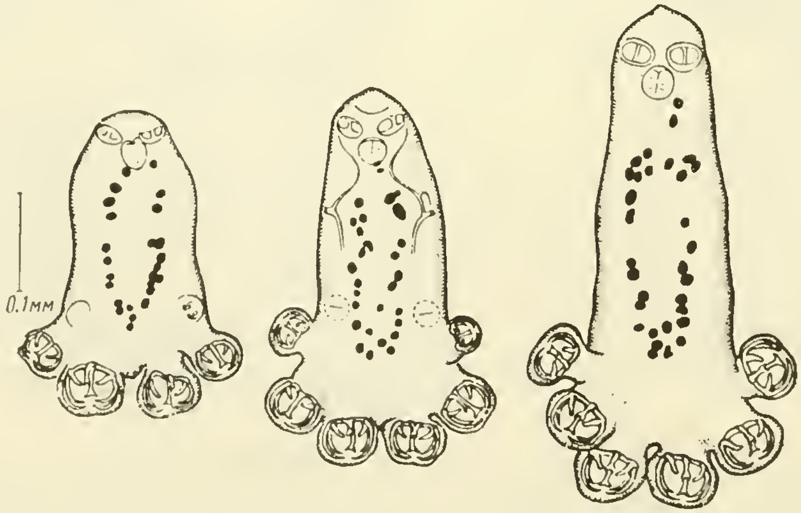

Fig. 256. Microcotyle gotoi Yamaguti, stages of development of young worms from the gills of Hexagrammos octogrammus (Pal.) from the region of Yablichnoii (southern Sakhalin, Sea of Japan).

remains on the posterior end of the larva (Fig. 255) which is quickly smoothed. The development of the internal organs proceeds slowly with the exception of the intestine. Already in the larva which has 2-3 pairs of clamps the latter forms 2 lobes extending into the posterior end of the body (Fig. 256). These grow very quickly and change into the intestinal trunks of the adult form. The sex system is developed considerably later. Approximately at the stage which has 13 to 16 pairs of attaching clamps one can observe the sex armature and considerable development of the sex glands; whereas among individuals with 8 pairs of attaching clamps the sex system has not yet been fully differentiated.

Microcotyle donavini Beneden and Hesse--In her resumé p. 214
Sproston indicates a rather early stage of the development of this type with only 12 pairs of clamps. The given stage of development still has middle hooks at the end of the disc which are absent in subsequent stages. Thus, the falling-off of the cercomere in the given species takes place during relatively late stages.

28. The development of Axine Abildgaard

The genus Axine (Fig. 8) is close to Microcotyle but differs by an asymmetrical disc located obliquely in relation to the longitudinal axis of the body. The preservation of the larval middle hooks lying in the middle of the single longitudinal row of attaching clamps is characteristic for the adult form.

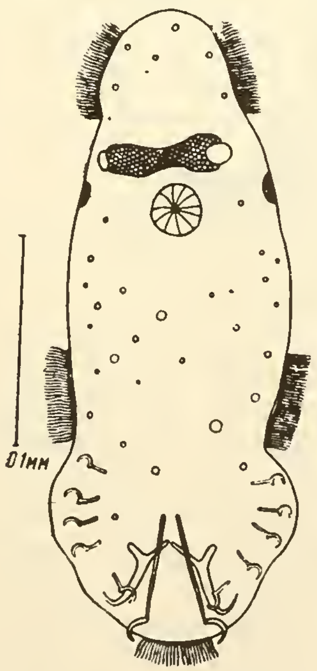

Fig. 257. Axine belones Abildgaard free-swimming larva. (Drawing from the preparation by U. A. Strelkov).

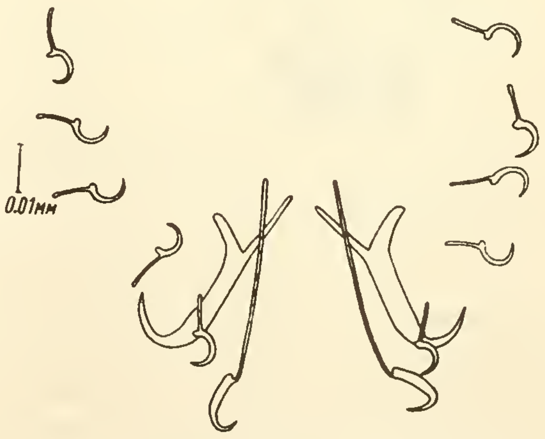

Fig. 258. Axine belones Abilgaard, attaching armature of the free-swimming larva.

During the time of his work at the Sebastopol Biological Station, U. A. Strelkov (Strelkov, 1953) hatched a free-swimming larva of Axine belones Abildgaard from the gills of Belone belone euxini (Gunther). In addition to that, during the 22nd cruise of the expeditionary vessel "Vityaz" in 1955 we obtained the development of two as yet undetermined species of Axine from the gills of flying fishes (Exocoetidae), which are conditionally designated by us as Axine sp. I and Axine sp. II. In the article of U. A. Strelkov the following description of the larva of A. belones Abildgaard is given: "The body of the larva is elongated, it is widened toward the posterior end where the attaching disc is located (Fig. 257--B. B.). The length of the body is 0.2 - 0.3 mm. The width is 0.5 - 0.8 mm. One double, pigmented eye is located in the anterior end. On the body of the latter one can clearly distinguish three zones of cilia. The first zone is located on the anterior end, the second in the middle part, the third on the posterior end of the body. The anterior ciliary zone is somewhat wider than the other two and reaches approximately the level of the eye. The second zone is somewhat narrower than p. 215 the first, and the third zone, lying on the posterior end of the attaching disc, is narrower than the two preceding zones. The attaching disc occupies about 1/3 of the body and bears 7 pairs of hooks of which 2 pairs are large middle hooks and 5 pairs are small lateral hooks (Fig. 258, B). The larger middle hooks are located along both sides of the mesial line of the body and have a different structure. The first pair resembles the middle hooks of Dactylogyrus in shape but with a larger handle. The length of the hook is 0.032 - 0.034 mm; the length of the point is 0.009 - 0.01 mm, the length of the handle is 0.012 - 0.014 mm, the second pair of hooks somewhat resembles the small edge hooks but is much larger. They have a thin, long straight handle and point. The average length is 0.035 - 0.044 mm, the length of the point is 0.008 - 0.011 mm. In the living

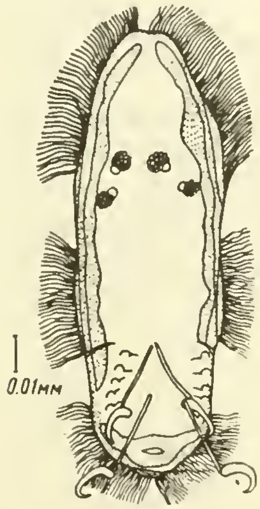

Fig. 259. Axine sp. I, free-swimming larva.

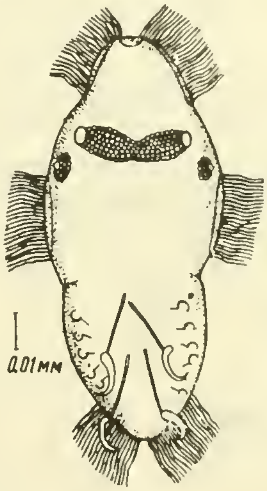

Fig. 260. Axine sp. II, free-swimming larva.

larva these hooks can extend beyond the limits of the attaching disc and apparently it is precisely by them that the larva first attaches to its host. The small edge hooks are located along the edges of the attaching disc and are so small that it is sometimes very difficult to notice them. They have a curved handle and a small point. The average length is 0.014 - 0.016 mm, the length of the point is 0.005 - 0.006 mm. In the middle part of the larva one can distinguish the inception of the intestine."

Just as his drawings, the description of U. A. Strelkov suffers by an apparent schematization. One must note two instances: first, that his enumeration of the middle hooks is the reverse of that accepted by us, i.e., the hooks, called by him as the first pair, correspond to our 2nd pair in the preceding descriptions. The second and more substantial circumstance is the fact that Strelkov did not pay any attention to the presence of another pair of eyes lying lower than the double eye represented by him. This error is a result of the fact that glycerin-jelly preparations contain strongly flattened worms. As a result the 2nd pair of eyes happened to be displaced almost to the edges of the body and gave the impression of p. 216 accumulations of pigment having no relation to eyes. Nevertheless they are undoubtedly eyes, which is confirmed by our data on Axine sp. I and Axine sp. II. The larva of these species of Axine are essentially very similar to that of A. belones Abildgaard (Figs. 259, 260) but differ basically by the fact that the first type has 4 clearly expressed eyes and the 2nd--3, of which the anterior is doubled--fused--and has 2 light refracting little lenses, whereas the 2 posterior are of normal structure. In such a fashion the representatives of the genus Axine have 3-4 eyes in the larval stage which completely disappear in the subsequent development (see page 402).

29. The development of Diplasiocotyle Sandars

In 1944 Sandars (Sandars) described a new species and genus of Microcotylidae from the gills of Agonostomus forsteri Cuv. and Val. from western Australia. According to the author this genus is characterized by differences in the structure of the attaching disc. It bears only 7 pairs of relatively large clamps and one small terminal (pair of clamps, nobis). Unfortunately we were not able to obtain the original work of the author and because of that have no way to judge the propriety of the establishment of this genus. The development of the given species is described in this work (I am indicating this according to the data which were cited in the resumé of Sproston). The larvae emerge on the 19th day after the deposition of eggs. They bear a ciliary covering which is located in three zones just as among Microcotyle. They resemble the larva of M. spinicirrus and have 2 pairs of middle hooks and 3 pairs of edge hooks on the attaching disc. The youngest worms discovered on the gills of the host have the length of 0.687 mm and a well-developed attaching disc having a diameter of 0.312 mm. The disc bears 4 pairs of attaching clamps and 2 pairs still in the process of development. The "larval attaching disc" with its middle and edge hooks is already absent by this stage of development.[1]

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[1] Supplement to the proofreading. In November, 1955, the work of Frankland /(Helga M. T. Frankland). "The life history and bionomics of Diclidophora denticulata (Trematoda: Monogenea). Parasitology 45, 3-4: 313-351/, in which is described in detail the development of D. denticulata starting from the development of eggs and terminating with the post-embryonic development on the gills of the host, appeared in print. The data of the author concerning the free-swimming larva coincide with ours with the exception that according to Frankland the general sizes of the larva as well as of the hook apparatus are two times smaller than the ones observed by us (see page 198). The reasons for this are not clear to us, however, judging by the drawing of Frankland the larvae were examined by her in fixed shape which probably caused the minimization of the true numbers (measurements, nobis). The subsequent stages of development described by Frankland are analogous to the ones observed by us in Microcotylidae (see page 210) and do not require special remarks. The remarks of Frankland concerning "ciliary larva" (loc. cit., pages 338-346), in which she indicates all the literary data known to her about free-swimming larvae are interesting. These data are reproduced in the corresponding places of the present appendage. It is noteworthy that the structure of the larva causes Frankland to indicate that there are two types of larvae , to the first of which are related the larvae of Monopisthocotylea and Polystomatoida from Polyopisthocotylea and to the second--only Diclidophoridea (should this be the superfamily -oidea?, nobis) (Polyopisthocotylea), i.e., the author unwillingly comes to the same inferences as we without drawing the corresponding conclusions from it.

PART II

OCCURRENCE
OF
MONOGENETIC TREMATODES
ON
THEIR HOSTS

Page Numbers In Margins Refer To Original Russian Text

PART II

OCCURRENCE OF MONOGENETIC TREMATODES ON THEIR HOSTS

CHAPTER I

HOSTS OF MONOGENETIC TREMATODES

As a rule monogenetic trematodes parasitize vertebrates. p. 219 Their discovery on cephalopods (Cephalopoda) and on isopods (Isopoda parasitica) appears to be an exception. Until this time only one monotypical genus *Isancistrum* Beauchamp (*I. loliginis* Beauchamp) from the gills of *Loligo vulgaris* L. and *L. media* L., which was encountered only once, is known. Those monogenetic trematodes parasitizing the Isopoda parasitica are related to the family of Diclidophoridae. They arouse a great interest because they indicate the possibility of a change toward superparasitism. However, it seems to us that here we deal not so much with the adaptation to a new group of hosts, a group strongly isolated from the preceding ones (isopods--fishes), but rather we deal with the adaptation to a new place of parasitizing on the same host, a place which also became a new host. If we remember that until the present time these parasites were found basically on the isopods living in the bodies of fishes and never in the free-swimming ones, this point of view will not appear paradoxical.

Among the vertebrates, the hosts of monogenetic trematodes appear to be mainly representatives of the three classes of fishes: shark-types (Elasmobranchii), full-headed-typed (Holocephali), and the highest fishes (Teleostomi), and to a much smaller degree on amphibians (Amphibia), and reptiles (Reptilia). As an exception one genus and species from an aquatic mammal is known, specifically *Oculotrema hippopotami*, described by Stunkard (Stunkard, 1924), from the eye of the hippopotamus from Africa. One must note with this that it is possible that the parasite was erroneously mistaken for a parasite parasitizing (another one which normally parasitizes, *nobis*) the hippopotamus, for judging by the work of Stunkard, the possibility of an error in labeling is not excluded[1], and by its structure *O. hippopotami* greatly resembles representatives of the genus *Polystomoides* Ward and (species, *nobis*) close to the latter.

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[1] In the work of Stunkard is indicated: "the material consists of 5 polystomes which have the label 'from the eye of hippopotamus.' It is probable that they were collected by the late professor A. Loss from the Nile hippopotamus from the Hij zoological garden in Cairo, Egypt, but unfortunately, there was no other information (on the label, *nobis*)".

In order to understand the nature of the distribution of the Monogenoidea on their hosts correctly and to evaluate the degree of their adaptability to the latter, we consider it useful to conduct an analysis of the occurrence of monogenetic trematodes on their hosts, and first of all, on the basic group--fishes. This analysis can be more easily conducted, starting from the evaluation of the occurrence of the species of Monogenoidea on the species and genera of their hosts--fishes, and only p. 220 then to transfer our attention to the characteristic correlation of larger taxonomic units of parasites with the large systematic subdivisions of their hosts. Such continuity will enable us to approach the question under consideration, and will further help to show the existing normal relations.

It is necessary to make a few preliminary remarks. The term "occurrence" as used by us is adopted in order to underline the principle difference between the natural distribution of parasites on their hosts which is observed in nature, and those potential possibilities toward the infection of "different" animals by parasites which can be discovered in experimental conditions or during certain disruptions of the natural process in nature (Pavlovsky, 1946). The term "specificity" so widely used at the present time in all cases of finding the parasite only on one host in nature without taking into consideration the repetition and of potential possibilities of infection should, in our opinion, be used with great reserve. Thus, we do not juxtapose occurrence with specificity but we consider that it is inadvisable to place the sign of equality between these two phenomena and that it is only the analysis of the nature of occurrence, as we shall further attempt to demonstrate, that can lead to the establishment of the degree, of specificity of various parasites in relation to their hosts.

The data about all the known monogenetic trematodes up to 1953 and certain supplemental data from recent times, serve as material for the composition of the following chapters. Also, in spite of a number of their shortcomings, the resumes of Sproston, (Sproston, 1946) and Price (Price, 1936-43) are basically used and they are supplemented by subsequent works, particularly by Russian and American researchers. Unfortunately, it is difficult to take into consideration a number of works for very different reasons, and thus undoubtedly there is a certain amount of data which has not been considered in our analysis, and because of this there are certain inevitable gaps. However, considering the total amount of factual data, the gaps are not so numerous, and further supplements and corrections cannot alter the general picture of the normalities (the dictionaries give normal, natural, law-governed, and, development in conformity with natural laws, as equivalents of the root of this Russian word. Its ending makes it a noun. We have translated it variously as generalization, principle, normality or regularity, depending on the sentence. See Foreword, nobis) which are obtained as a result of this analysis.

Before speaking about the distribution of Monogenoidea, one must point to the considerable difficulties connected with the correct determination of the host of the parasites--that is, on the first order--fishes. On this, in considerable measure, depends the correctness of the subsequent conclusions. Unfortunately, in this connection one must consider the data of a number of authors with great reservation. Equally sad, and what also impedes the work, is the fact that in many works, especially of the past century, the same fishes are cited under different species names. This condition is worsened by the confusion of synonyms of certain groups of fishes which even an ichthyologist finds difficult to untangle.

The system of fishes and their division into orders were taken by us from the work of L. C. Berg (1940) but with two changes. Thus, L. C. Berg takes tunas (Thunnidae) as a special order--Thunniformes; we on the other hand, in conformity with the opinion of the majority of contemporary ichthyologists, refer this order to the perch-bass family (Perciformes, nobis) placing it close to Cybiidae (in the understanding of L. B. Berg). L. C. Berg also speaks about the proximity of tuna with the latter in his work.

In addition to that, instead of the decimal system which divides contemporary Selachii into 6 orders as is accepted by L. C. Berg, we consider it more convenient to recognize all Selachii as one order--Selachiiformes, in conformity with the opinion of G. V. Nikolsky (1954).

This work is considerably hampered by the absence of well-developed broad, but detailed phylogenetic schemes for fishes. Further, in addition to the system of L. C. Berg, which bears a rather formal character according to our conviction, we have utilized a number of papers which will be referred to in appropriate places. For the time being, we shall only note that the scheme of interrelations of the bony fishes of Gregory (Gregory, 1951) gave us very many useful indications for further systematizations and apparently has much that is logical in its foundations. Parasitological data connected with this will be expressed somewhat later. We consciously avoid speaking now about the general theoretical questions connected with the problem of occurrence and specificity of parasitic animals, considering that for their useful discussion it is indispensable to express the factual material first. p. 221

CHAPTER II

OCCURRENCE OF SPECIES OF MONOGENETIC TREMATODES ON THE SPECIES AND GENERA OF THEIR HOSTS--FISHES

The data concerning the occurrence of the 958 species of p. 222 monogenetic trematodes known to us at the present time, composed on the basis of literary sources (including our own works), are represented in Table IV. Examining them we see that 806 species or 84.1 % of the total number of monogenetic trematodes are encountered on representatives of one genus of fishes. Those discovered on two genera of fishes are indicated as 100 species or 10.4%, on three genera of fishes--30 species or 3.2%, and finally on four and more genera of fishes--22 species or 2.3% species of Monogenoidea. Thus only 152 species of monogenetic trematodes, that is 15.9% of their total number, are encountered on other than one genus of fishes, a fact which in itself indicates the strong adaptation of the worms to their hosts. Furthermore, as is seen from the table, among the ones (hosts, *nobis*) related to the same family, that is, indisputably related with each other, 903 species of monogenetic trematodes are encountered on 94.2% and only less than 6% are encountered as parasitizing species of different families of fishes. If one takes into consideration that from the latter number more than two-thirds were found on fishes of one order, that is--fishes which are distantly related to each other, so to speak, then all these numbers underscore still more the high adaptation of the species of monogenetic trematodes to the genera and species of their hosts--fishes.

In connection with the above-mentioned, special interest is occasioned by the cases in which monogenetic trematodes are indicated as occurring on several fishes of different families, and especially those that occur on a large number of species belonging to different families of various orders of fishes. In order to understand and evaluate these cases, let us get acquainted more in detail with each one of them.

Five species of monogenetic trematodes specifically: *Ancyrocephalus alatus* Chauhan, *Gyrodactylus arcuatus* Bychowsky, *Benedenia melleni* (MacCallum), *Tristoma coccineum* Cuvier, and "*Cyclocotyla*" *bellones* Otto are indicated on more than three species and genera of different orders.

Ancyrocephalus alatus was described by Chauhan (Chauhan, 1945) from *Muraenesox talabanoides* Bleck. (Muraenesocidae, Anguilliformes), *Arius falcarius* Rich. (Ariidae, Cypriniformes), *Mugil parsia* Bleck. (Mugilidae, Mugiliformes), and *Harpodon neherius* Ham. and Buch. (Scopelidae, Scopeliformes). Chauhan writes that the first host was the most infected, each of the specimens examined had individual *Anc. alatus* on the gills. One can thus consider that *Muraenesox*

TABLE 4

Occurrence of Species of Monogenetic Trematodes on Fishes

Number of species of Monogenoidea	On 1 species of fishes	On 2 species of fishes	On 3 species of fishes	On more than three species of fishes	Total
On species of 1 genus of fishes	711	78	13	4	806
On species of 2 genera of 1 family of fishes		49	15	9	73
On species of 3 genera of 1 family of fishes			8	4	12
On species of more than 3 genera of 1 family of fishes				12	12
On species of 2 genera of different families of 1 order of fishes		13	3	3	19
On species of 3 genera of different families of 1 order of fishes			8	5	13
On fishes of more than 3 genera of different families of 1 order of fishes				5	5
On species of 2 genera of different families and orders of fishes		6	1	1	8
On species of 3 genera of different families and orders of fishes			5		5
On species of more than 3 genera of different families and orders of fishes				5	5
TOTAL	711	146	53	48	958

talabanoides is the chief host of this species. It is impossible to say anything definite regarding the occurrence of the other species of fishes which were indicated until secondary findings substantiating the data of p. 223 Chauhan are made. Our certain suspicion toward the data reproduced is caused by the fact that in the works of Chauhan there are, as we will show later, a number of dubious indications about hosts of separate parasites (see pages 227, 228 and others).

Gyrodactylus arcuatus arcuatus, which was encountered many times by different researchers, was first described by us from *Pygosteus pungitius* (L.), and *Gastrosteus aculeatus* L. (Gasterosteidae, Gasterosteiformes). In addition to that, the special subspecies--*Gyrodactylus arcuatus gerdi* Bychowsky from *Eleginus navaga* (Pall.) and *G. arcuatus proximus* Kutikowa from *Boreogadus saida* (Lep.) (Gadidae, Gadiformes), were discovered (Bychowsky, 1933b). The two last subspecies are closer to each other than to the typical species, which is undoubtedly connected to their occurrence on representatives of one family (standing far from the family which *G. arcuatus arcuatus* parasitizes). The transfer of the latter to the fishes which are far removed from the initial host is probably linked with the relative phylogenetic youth of the species, and because of that--with a weaker adaptation to the host. This is also underlined by the circumstance that the given species is encountered both in fresh and in marine waters--on the transitory just as on the truly fresh water or purely marine hosts, (Bychowsky and Poljansky, 1953; Shulmann and Shulmann--Albova, 1953).

Benedenia melleni was first described by MacCallum from the New York Aquarium, "from the eyes of *Sphaeroides annulatus*, *Chaetodipterus faber*, *Angelichtyes isabelita*, *Pomacanthus arcuatus*, etc." (MacCallum, 1927). The author supposed that this parasite was p. 224 carried to the aquarium with the first of the above-mentioned species of fishes from California, that is, of Pacific Ocean origin and that it transfered to the other hosts only in the artificial conditions. However, this does not correspond to reality. Thus, Jahn and Kuhn (Jahn and Kuhn, 1932) indicated that according to the opinions of the workers in the New York Aquarium at the time when *B. melleni* appeared in the aquarium there were no *Sphaeroides annulatus* in it and that the parasite mentioned was brought and is brought into the bodies of water not by fishes of the Pacific Ocean but from the Atlantic Ocean--from West India (from the region of the Bahama Islands). At the present time one can consider it fully substantiated that *B. melleni* was discovered on a number of fishes in the region of Bimini Island in natural conditions (Nigrelli, 1947). At the present time *B. melleni* is known from the following fishes in natural artificial bodies of water:[1]

Beryciformes

Holocentridae:
Holocentrus _ascensionis_ (Osbeck).

Serranidae:
Centropristis _striatus_ (L.)
Dermatolepis _punctatus_ Gill.
Epinephelus _adsensionus_ (Osbeck)
_E._ _guttatus_ (L.)
_E._ _morio_ (Cuv. et Val.)
*_E._ _striatus_ (Bloch.).
Paralabrax. _maculatofasciatus_ (Steind.).
Promicrops _itaiara_ (Licht.).

Malacanthidae:
Malacanthus _plumieri_ (Bloch.).

Pomatomidae:
Pomatomus _saltatrix_ (L.).

Carangidae:
Caranx _crysos_ (Mitch.).
_C._ _hippos_ (L.)
Naucrates _ductor_ (L.)
Trachinotus _carolinus_ (L.)
_T._ _glaucus_ (Bloch.).
_T._ _goodei_ Jord. et Everm.
Vomer _setapinnis_ (Mitch.).

Lutianidae:
Lutianus _analis_ (Cuv. et Val.)
*_L._ _apodus_ (Walb.).
_L._ _jocu_ (Bloch. et Schn.).
_L._ _synagris_ (L.).

Pomadazyidae:
Anisotremus _surinamensis_ (Bloch.).
_A._ _virginicus_ (L.).
Haemulon _album_ Cuv. et Val.

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[1] In the list the species on which _B._ _melleni_ is encountered in nature are marked by an asterisk.

Sciaenidae:

Menticirrhus saxatilis (Bloch. et Schn.)
Micropogon undulatus L.

Ephippidae:

Chaetodipterus faber (Brous.).

Chaetodontidae:

Angelichthys ciliaris (L.).
A. isabelita Jord. et Rut.
A. townsendi Nich. et Mowb.
*Chaetodon ocellatus Bloch.
*Ch. striatus L.
*Ch. capistratus L.
*Pomacanthus arcuatus (L.).
*P. paru (Bloch.).
Holacanthus strigatus Gill.
*H. ciliaris L.
*H. tricolor (Bloch.).

Labridae:

Lachnolaimus maximus (Walb.)
Tautoga onitis (L.)

Acanthuridae:

Acanthurus caeruleus Bloch. et Schneid.
A. hepatus (L.)

Triglidae:

Prionotus evolans (L.).

Tetrodontiformes

Balistidae:

Balistes vetula L.
Melichthys bispinosus Gilb.
M. piceus (Posy).
Alutera scripta (Osbeck)
Ceratacanthus schoepfi (Walb.).
Stephanolepis hispidus (L.)

Ostraciidae:

Lactophrys tricornis (L.)
L. trigonus (L.)
L. triqueter (L.).
L. bicaudalis (L.).

Tetrodontidae:

Sphaeroides annulatus (Jen.).
S. maculatus (Bloch et Schneid.).

Diodontidae:

Diodon hystrix L.

p. 225 Thus we see that in natural conditions this species is encountered only on the perch-bass family (Perciformes, *nobis*) and basically on Chaetodontidae. In aquarium conditions, i.e., in relatively crowded conditions, 48 more species are infected in addition to the above-noted nine species of the perciformes type. These are related to 17 families of three orders of fishes. In the opinion of the majority of the ichthyologists, the relation between these orders is undoubtedly consanguinous. Thus, Nikolsky (1954) writes that, "there are many bases for considering Beryciformes as a group which is initial (hereditarily ancestral, *nobis*) for the perca-type (Perciformes, *nobis*)." In the system of fishes of L. C. Berg (1940) it is indicated that Tetrodontiformes are connected through Acanthuridae with the Perciformes. In the scheme of phylogenetic relations of bony fishes in the work of Gregory (Gregory, 1951) the connections between all three orders (Berycoidei, Acanthopterygii, in the narrow sense, and Plectognathi--according to the terminology of Gregory) are fully apparent. Thus, contrary to the two preceding cases and in spite of the huge number of hosts, *B. melleni* nevertheless parasitizes (only, *nobis*) more or less related groups of fishes. This circumstance is especially indicated by the fact that in the New York Aquarium, where together with the infected fishes,others were kept as well, Elasmobranchii (sharks as well as skates) were never infected, and among Teleostomi--the representatives of Anguilliformes (Muraenidae), Cyprinodontiformes (Poeciliidae), Syngnathiformes (Syngnathidae), Echeneiformes (Echeneidae), and Batrachoidiformes (Batrachoididae) were never infected.

Tristoma coccineum is indicated from the perciformids, *Xiphias gladius* L. (Xiphiidae), and *Tetrapturus belone* Raf. (Histiophoridae), for the shark *Sphyrna zygaena* (L.) (Sphyrnidae) and for Moonfish (Ocean Sunfish, *nobis*) (Molidae, Tetrodontiformes). It is difficult to say anything precise on the subject of the occurrence of this species; however, we suppose that indications to its finding on the Moonfish pertain not to this species but to *Tristoma papillosum* Diesing. The majority of the contemporary authors identify the latter type with *Tr. coccineum* which is hardly justifiable (Sproston, 1946). Thus,it is more probable that the given species is encountered only in the two closely related families Xiphiidae and Histiophoridae and the completely unrelated family Sphyrnidae.

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"*Cyclocotyla*" *bellones* was described from the skin of *Belone belone* (Brun) (the Hornhecht, according to Otto 1823), Price (Price, 1943a) took this species for the type of the genus and included it in the majority of species placed by Sproston (Sproston, 1946) in the genus *Choricotyle*. Along with this, Palombi (Palombi, 1943b, 1949) placed *C. bellones* in the genus *Diclidophora*, which is understood very broadly by him, and entered *Choricotyle smaris* Ijima, in Goto 1894, *Ch. squillarum* (Parona and Perugia) and *Ch. charicoti* Dollfus into the synonymy of the given species. One can hardly agree with the opinions of Price and Palombi and it is more correct to consider this genus and species as *genus et species inquirendum* as is done by Sproston, in our opinion, quite correctly so. Actually, *C. bellones* was found only once and thus even though Palombi indicates a number of perciformids besides *Belone* as hosts of this species, these data cannot now be accepted. Hence, *C. belones* must be excluded from the corresponding group in Table 4 and transferred into the group discovered only on one species.

Five species of monogenetic trematodes--*Tristoma integrum* Diesing, *Tr. papillosum* Diesing, *Diplectanotrema balistes* (MacCallum), *Diclidophora palmata* (Leuckart) and *D. merlangi* (Kuhn)--are indicated on three species of fishes related to three various genera of different families and orders.

Tristoma integrum was described from *Xiphias gladius* L. (Xiphiidae, Perciformes) on which it has been also often found subsequently. In addition to that Palombi (Palombi, 1949) indicates as hosts of this species (on the basis of the data of Italian researchers and his own p. 226
opinion that *Tr. coccineum* of a number of authors and *Tr. rotundum* are synonyms of the species under consideration) also *Tetrapterus belone* Raf. (Histiophoridae, Perciformes) and *Mola mola* L. (Molidae, Tetrodontiformes). The opinion of Palombi is clearly insufficiently supported, in connection with which it is more correct to consider that at the present time Tr. integrum is known only from one species of hosts and consequently does not belong in the group considered in Table 4.

Tr. papillosum is indicated also on the same three species of hosts as the preceding species. It is not considered possible to establish the correctness of these data. We shall note, however, that Diesing (Diesing, 1836) indicated *Mola mola* as the first host of this species. Generally one must say that the synonymy of the genus *Tristoma* and the independence of its separate species demands special research. Thus, *Tr. papillosum* must be (for the present, *nobis*) considered as occurring on the hosts indicated, of which two-*Xiphias* and *Tetrapterus*, belong to families closely related to each other, whereas the third is considerably removed from the first.

Diplectanotrema balistes is indicated from *Balistes capriscus* Gm. (=*B. carolinensis* Gm) (Balistidae, Tetrodontiformes), *Acanthurus* (=*Teuthis*) *hepatus* (L.) (Acanthuridae, Perciformes), and *Anisotremus virginicus* (L.) (Pomadasyidae, Perciformes). At first it was described as *Diplectanum balistes* by MacCallum in 1915 from the first host and then in 1916 also by him under a different name (*D. plurovitellum*) from two other fishes. Later Johnston and Teigs (Johnston and Tiegs, 1922) isolated *D. plurovitellum* into the special genus Diplectanotrema, whereas Price (Price, 1937c) made *D. plurovitellum* synonymous with *D. balistes*, preserving the new name of the genus. As a result, if one is to recognize the opinion of Price about the conspecificity of both species[1] we must consider that *D. balistes* are encountered on the fishes of two orders. With this one cannot fail to note that in spite of the fact that they are related to two different orders (see page 270) Balistidae and Acanthuridae are closer to each other than the last family is to Pomadasyidae although they are both Perciformes, that is related to each other in some degree. One must also explain that in all cases of the finding of *D. balistes* the fishes were taken from the New York Aquarium, i. e., from artificial conditions where the possibility of more wide infection than occurs in nature is not excluded.

In the literature *Diclidophora palmata* is indicated on *Molva molva* (L.), *Gadus morrhua* L. (Gadidae, Gadiformes)[2] and *Hippoglossus hippoglossus* (L.) (Bothidae, Pleuronectiformes). During verification the indications of the finding (of this parasite, *nobis*) on the two last species were found to be inexact. Thus the reference of Sproston (Sproston, 1946)

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[1] It seems to us that in the given case Price is mistaken and MacCallum correctly divides these two species. The structure of the vitellaria in *D. plurovitellum* is so characteristic that it alone distinguishes the given species from *D. balistes*. The references to poor preparations (Price, 1937c) are without foundation, because during fixation and in any condition of the subject the shape of the vitellaria such as it is among *D. balistes*, is similar to the one among all lowest Monogenoidea, and it cannot change to such an extent as to become similar to the one possessed by *D. plurovitellum* which MacCallum and Price picture the same. Thus it is more probable that we deal here with two species of which one is encountered on the syngnathids and the second on the perciformids.

[2] Indication of the finding of *D. palmata* on *Odontogadus merlangus* (L.) (Stiles and Hassal, 1908), which has not been substantiated by any one as yet, has not been taken into consideration by us.

to Leuckart, 1842 is not correct. According to Sproston, Leuckart indicates the Cod --*Gadus morrhua* as a host of *Octobothrium* (=*Diclidophora*) *palmatum*, whereas actually in the works cited the question is about *Gadus molvae*, that is *Molva molva*, which is the common host of *D. palmata*. The question about the finding of this genus on *Hippoglossus hippoglossus* p. 227
is more complex. The data of Rathke (Rathke, 1843) about the finding of the parasite which was described by him as the new species, *Octobothrium digitatum* Rathke on the Paltus serve as a basis for this indication. In his "Systema Helminthum" Diesing (Diesing, 1850) placed this species as synonymous to *D. palmata* without any explanation. Until the present time this has been accepted by all authors as the actual relations in spite of the fact that no one ever found *D. palamata* on the Paltus just as (they found no, *nobis*) other species of this genus. We find the only indication of certain doubt concerning these deductions in the work of Cerfontaine (Cerfontaine, 1895b) where the opinion of Van Beneden, who considers it unlikely that the worms discovered by Rathke on the Paltus refer to *D. palmata*, is reproduced in a footnote. We consider the opinion of Van Beneden completely correct in that one must not make *Octobothrium digitatum* Rathke synonymous with *D. palmata* (Leuckart). For the time being this species must be left without precise generic identification but as independent though demanding redescription after new findings. We think that during verification it will appear to be more likely as a representative of the genus *Heterobothrium* or of one close to it. Thus, *D. palmata* must be placed with the group of species which are encountered on one species of host and not on several and especially of different orders.

In the literature, *Diclidophora merlangi* is indicated from the gills of *Odontogadus merlangus* (L.) and *Micromesistius poutassou* (Risso) (Gadidae, Gadiformes), and also from the isopod *Cymothoa oestroides* Risso from the buccal cavity of *Box boops* (L.) (Sparidae, Perciformes). One can definitely consider the last indication as erroneous, for the structure of the attaching disc of *D. merlangi* does not permit this species to attach to the body of isopods and thus there is a mistake here in classification. As regards the finding of *D. merlangi* on *Micromesistius*, it is more probable that here mistaken classification has also occurred [usually a close host]. species--*D. minor* (Olsson)--is encountered on the last host . However, if one is to recognize the correctness of the corresponding data both species of hosts are related to close genera of the same family. Hence, *D. merlangi* must be considered as existing either on two close genera or even on one species of host.

Only *Calicotyle kroyeri* Diesing is indicated on many species of fishes of two genera related to different orders. It is indicated on a whole series of species of *Raja* (Rajidae, Rajiformes) and on *Rhombus maximus* (L.) (Bothidae, Pleuronectiformes).[1] The only indication pointing to the last host is contained in the supplement to the resume of St. Remy (St. Remy, 1898) where it is written that *C. kroyeri* is encountered on the skin of *Rhombus maximus* in addition to *Raja* species. Our attempts to find the bases for these data were not successful. Consequently, apparently there is some mistake, if it isn't in the materials of St. Remy themselves. The latter, as a matter of fact, is improbable. (It is unlikely that there was a mistake in the writing or compiling of the material by St. Remy, but the error occurred somewhere else, *nobis.*) Therefore, this species must be considered as being encountered only on the representatives of one genus of skates.

Squamodiscus belengeri Chauhan is described by the author of the species from three species of fishes of two genera of different orders, specifically: from *Sciaena belengeri* (Cuv. and Val.), *S. carutta* (Bloch.) (Sciaenidae, Perciformes), *Muraenesox talabonoides* Bleck. (Muraenidae, Anguilliformes). The accuracy of these indications of the finding of *S. belengeri* on the last host arouses doubt because it is possible that here there was a mistake in labeling or the worms came onto the gills of *Muraenesox talabonoides* from a devoured *Sciaena.* (Similar cases were discovered by us for a number of *Dactylogyridae*). In any case, for the p. 228
time being, one must consider only the *Sciaena* spp. as the characteristic hosts of S. *belengeri* and until the substantiation of the data about *Muraenesox*, one should not take the latter into consideration.

Six species of monogenetic trematodes are indicated on two species of fishes related to different orders: *Bilaterocotyle chirocentrosus* (Chauhan), *Calicotyle affinis* Scott, *Dionchus remorae* (MacCallum), *Microbothrium apiculatum* Olsson, *Urocleidus mimus* Mueller, and *Squalonchocotyle mavori* (Linton).

Bilaterocotyle chirocentrosus was described by Chauhan (Chauhan, 1945) from *Sciaena belengeri* (Cuv. and Val.) (Sciaenidae, Perciformes) and *Chirocentrosus dorab* Forsk. (Chirocentridae, Clupeiformes). Seven specimens of worms were encountered on the first host and on the second, only one. As we see we encounter for the first time the data of the same researcher which arouse doubts in some degree. Running ahead, we shall indicate that for the entire family of Protomicrocotylidae, to which *Bilaterocotyle* is related, occurrence on the herring types (Clupeiformes, *nobis*) is unknown, with the exception of one case, which confirms our conviction that the finding of *B. chirocentrosus* on

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[1] The indications of Ruszkowski (Ruszkowski, 1934) of the finding of this species on *Chimaera monstrosa* L., which is also reproduced in the resume of Sproston, is erroneous and related to another species as Brinkmann (Brinkmann, 1952a) has indicated.

Chirocentrosus dorab is accidental and that this species of monogenetic trematode must be considered characteristic only for Sciaenidae.

Calicotyle affinis is encountered very often on *Chimaera monstrosa* L. (Chimaeridae, Chimaeriformes) and, although rarely, without any doubt on *Raja fullonica* L. (Rajidae, Rajiformes) (Brinkmann, 1940, 1952a).

Dionchus remorae is indicated only for *Echeneis naucrates* L. (Echeneidae, Echeneiformes) and *Caranx hippos* L. (Carangidae, Perciformes). According to Regan, Echeneiformes could originate from forms related to Carangidae (See Berg, 1940) and, thus, the finding of the same species of monogenetic trematodes on representatives of these two families underlies their consanguine ties, especially since the second species *Dionchus agassizi* Goto is encountered only on Echeneidae [*Remora remora* (L.), *R. brachypterus* L.]. During the discussion of the above-mentioned (possibility, *nobis*) with us, L. C. Berg considered it so interesting that he even advised us to publish a special article on the subject (see further page 256).

Microbothrium apiculatum has been described several times and is encountered on *Squalus acanthias* L. (Squalidae) and in addition to that is described by MacCallum (MacCallum, 1926) on *Carcharhinus commersonii* Blanv. (Carcharhinidae). Thus, this species of monogenetic trematode parasitizes representatives of two families of sharks which are very distant from each other.

Urocleidus mimus was encountered by Mueller, the author of type, on *Esox niger* Le Sueur (Esocidae, Clupeiformes) and *Lepibema chrysops* (Raf.) (Serranidae, Perciformes). Subsequently this species was discovered for the second time in larger quantity on the second host (Mizelle and Klucka, 1953). In her resumé Sproston cites *Lepibema* for some reason with a question mark, although it would have been more correct to place the question mark before *Esox*, the finding on which is undoubtedly accidental, (if it were otherwise, the finding on *Esox* would have been substantiated during the extensive research of Mizelle and his co-workers) and is possibly explained by the fact that the worms came to the pike from a devoured host.

Squalonchocotyle mavori was described by Linton (Linton, 1940), who indicated that the worms of this species were discovered on the bottom of an aquarium which contained individuals of *Morone americana* (Gmel.) (Serranidae, Perciformes). At the same time he correctly in- p. 229
dicated doubt of the fact that these fishes could be the true hosts of the given species. Sproston in her resumé (Sproston, 1946) indicates that Price in his work in 1942 established a new host for *S. mavori*--*Sphyrna zygaena* (L.) (Sphyrnidae, Selachiformes). This is absolutely untrue

because in the work of Price there are no indications whatsoever on the subject and in addition he correctly considers it impossible to recognize the representatives of Perciformes as the host of *S. mavori* and supposes that such (the host, *nobis*) must be some shark, hence the necessity of excluding the species under consideration from the group of those which parasitize representatives of two different orders of fishes and to transfer it into the group with one host.

In conclusion of our analysis of the 18 species of monogenetic trematodes indicated as parasitizing different orders of fishes one must exclude as incorrectly placed in this group of species the following:

(1) *Diclidophora palmata* (Leuckart), *Tristoma integrum* Diesing, *Squalonchocotyle mavori* (Linton), and *Cyclocotyla bellones* Otto--actually they appear only on one species of host;

(2) *Calicotyle kroyeri* Diesing is encountered only on representatives of one genus of fishes;

(3) *Diclidophora merlangi* (Kuhn) parasitizes representatives of two genera of one family of fishes or even one species.

Further one must consider the relation of the following four species to the given group as doubtful: *Ancyrocephalus alatus* Chauhan, *Squamodiscus belengeri* Chauhan, *Bilaterocotyle chirocentrosus* (Chauhan) and *Urocleidus mimus* Mueller. The first three are described by Chauhan and his data about the hosts are doubtful and require special verification. With a great degree of probability,one can consider that *Squamodiscus belengeri* and *Bilaterocotyle chirocentrosus* parasitize only Sciaenidae and are encountered only accidentally on other hosts. As regards *Urocleidus mimus*, the latter species apparently is encountered only on one species of host, which agrees with the subsequent data as we will see further (see page 350).

Four species are encountered on fishes which are related in some degree, although belonging to different orders: *Benedenia melleni* (MacCallum), ? *Diplectanotrema balistes* (MacCallum), *Dionchus remorae* (MacCallum), and *Microbothrium apiculatum* Olsson. One can consider as linked to this group the two species of *Tristoma* examined here--*Tr. coccineum* Couvier and *Tr. papillosum* Diesing of which each is encountered on two closely related families of Perciformes and on one family of Tetrodontiformes, which are undoubtedly linked phylogenetically with the preceding order, although somewhat remotely. Finally only two species are encountered on orders of fishes unrelated to each other, specifically--*Calicotyle affinis* Scott and *Gyrodactylus arcuatus* Bychowsky. We will return later to these two species.

We pass now to the examination of monogenetic trematodes which are indicated as parasitizing different families of fishes which, however, are related to the same order.

Five species of monogenetic trematodes are indicated as parasitizing four or more species of fishes related to different families of the same order: Capsala laevis (Verrill), Diplozoon paradoxum Nordmann, Discocotyle sagittata (Leuckart), Hexostoma grossum (Goto), and Microcotyle pomacanthi MacCallum.

Capsala laevis is encountered on several species of Histiophorus and Tetrapturus (Histiophoridae) and then on Xiphias gladius (L.) (Xiphiidae) and finally on p. 23
Coryphaena hippurus (L.) (Coryphaenidae). All three families are undoubtedly related to each other (Gregory places them in Scombrodei).

Diplozoon paradoxum is known from more than 30 species of various Cyprinidae and from several species of Cobitidae. Both these families are closely related. It is true that in the literature there are still a number of data concerning the finding of D. paradoxum on different fishes of other families or even orders which were not taken into consideration by us during the composition of Table 4. However, during the verification (these were found to be, nobis) probably erroneous. Thus, in the work of Wagener (Wagener, 1857a), the indication of the pike as a host of D. paradoxum is based on the finding of the egg and not the worm itself on the gills of Esox lucius L. The finding on the Ling (given in the Russian as Burbot, Eelpout--Lota, nobis) is indicated by Luhe (Luhe, 1909) was not substantiated by any other literary indications. Concerning Cottus gobio L. --there are data in the work of Hausmann (Hausmann, 1897) based apparently on accidental findings. Finally, the data about sticklebacks as hosts of D. paradoxum cited by Sproston (Sproston, 1946) are clearly incorrect. Numerous researchers in our laboratory and particularly in the Laboratory of Fish Diseases of VNIORH speak with certainty that D. paradoxum does not parasitize any fishes except representatives of the two above-mentioned families.

Discocotyle sagittata is encountered undoubtedly in a number of species of the genera of Salmo, Salvelinus and Coregonus (Salmonidae) and on Thymallus thymallus (L.) (Thymallidae). Both families of hosts are undoubtedly closely related, and Thymallidae have only recently been separated from Salmonidae as an independent family (Suvorov, 1948).

Hexostoma grossum was discovered on several representatives of Thunnidae and was indicated for the carangid Seriola aurevittata Tem. and Sch. (=S. quinqueradiata auct.). The latter arouses certain doubt in us, but if we consider that the data of Ishii and Sawada (Ishii and Sawada, 1938a) are correct, they reflect the views on genetic links or ties of Thunniformes with other Perciformes. Thus, the majority of ichthyologists consider Thunnidae closely linked to Scombroidei (Scombridae, Cybiidae, and others), and the latter genetically, "are undoubtedly linked with the lowest Percoidei and particularly perhaps originate from Carangidae." (Nikolski, 1954). Gregory on the other hand simply includes Carangidae in the group of Scombroidei (Gregory, 1951).

Finally, Microcotyle pomacanthi is listed by MacCallum as being encountered on three species of Chaetodontidae and one species of Sparidae, Serranidae, Pomadasiidae, and Labridae. All these families are related to the Perciformes although the degree of their consanguinous relations is very different. Thus, the first four families are related to the superfamily Percoidae. And the last family, Labridae, is related to the same suborder, Percoidei, but to a special superfamily Labroidae, i.e., it is rather more distant from the first (group of families, nobis) than they are from each other.

Five species of monogenetic trematodes are known from four or more species of fishes related to three genera of different families of one order.

The first of these species, Cathariotrema selachii (MacCallum) is encountered on two species of Carcharhinus (Carcharhinidae) and besides on Sphyrna zygaena (L.) (Sphyrnidae) and Alopias vulpinus (Bon.) (Lamnidae). All three families are related to the order Lamniformes and are undoubtdly consanguinous and represent one branch of the development of sharks (Suvorov, 1948).

The second species Tetraonchus borealis Olsson, is encountered on two species of Salmonidae and two species of Thymallidae. The subject of the consanguinous relationships of these two families of fishes was con- p. 231
sidered during the discussion of the occurrence of Discocotyle sagittata.

The third species--Gyrodactylus nemachili Bychowsky was discovered on a number of species of Nemachilis (Cobitidae) and on three species of carp-type fishes--Schizothorax pseudaksaiensis (Herz.), Sch. argentatus (Kessl.) and Phoxinus brachiurus Berg. In the work of Gvozdev, Agapova and Martehov (1953), in addition to that, the finding of G. nemachili on the perciformid fish Balarsch (in one individual) was also indicated, but we do not take into consideration this indication that this worm was accidentally transferred to the rapacious fish (perhaps it should read, we do consider that this worm was accidentally transferred to the rapacious fish? nobis). The finding on Cyprinidae is obviously not accidental because we (Bychowsky, 1936b) discovered G. nemachili on Sch. pseudaksaiensis, true only on one individual, but then the authors indicated above discovered this type on the Golian (the Phoxinus sp., nobis) in 61.8% of the fishes and on two species of Marinka, in one individual each. The relations between Cobitidae and Cyprinidae are undoubtedly close, as has been indicated.

The fourth species, Amphibdella maccallumi (Johnston and Tiegs), is indicated from four species of fishes of which three are related to two close genera of Torpedinidae and one (Squalus acanthias L.) to Squalidae. We have no doubt that the data about the last host are erroneous and consequently A. maccallumi must be considered as encountered on two genera of the same family of fishes. As a basis for this serves the fact that the information about the finding of this species on Squalus acanthias is based on the data of MacCallum and in the work where he describes this species for the first time, only one host--Tetranarce occidentalis (Storer) is indicated (MacCallum, 1916a). As was mentioned earlier, the data of MacCallum often do not deserve attention--in his work the faults of labeling are numerous and in this case this is very probable.

The fifth species, Axine belones Abildgaard, is only known with certainty from one species of host. Belone belone (L.), and is also indicated by Palombi (Palombi, 1949) from the gills of Tylosurus (=Belone) imperialis Raf., Exocoetus rondeleti, Cm., and Hexocoetus heterurus L. It is possible that Palombi is right, but it is more probable that he was dealing with several species of Axine, very close to each other, each parasitizing a different species of host. Our research on the genus Axine during the time of the 22nd cruise of the Expeditionary Vessel "Vityaz" in the Pacific Ocean in 1955 serves as a basis for such an opinion. These researches showed that a number of close but independent species, each of which is adapted to a very narrow circle of hosts and to only one species of fishes, parasitize Exocoetidae and Belonidae.

According to the literary data eight species of monogenetic trematodes parasitize three species of fishes related to three genera of different families but of one order: Ancyrocephalus manilensis Tubangui, A. mogurndae (Yamaguti), Ancylodiscoides varicus Achmerov, Encotyllabe spari Yamaguti, Heterocotyle minima (MacCallum), Thaumatocotyle dasybatis (MacCallum), Squalonchocotyle abbreviata (Olsson), and Sq. grisea Cerfontaine.

According to the data of the author who described it, Ancyrocephalus manilensis is encountered on three families of the perciformid group--Acanthuridae (typical host according to the author), Lutianidae, and Serranidae. Unfortunately we did not see the works of Tubangui (Tubangui, 1931)[1]. Sproston (Sproston, 1946) indicates that in the aquarium

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[1] We only had an extract from the text of the work describing the worm itself.

of the Scientific Bureau of Manila this parasite caused deaths of the hosts. It is possible,consequently,that A. manilensis was not discovered in natural p. 232
conditions. Even though they are related in the wide sense of the word, all three of the indicated families of fishes are, nevertheless, somewhat distant from each other.

Ancyrocephalus mogurndae was encountered in the beginning on two fresh water fishes--Mogurnda obscura (Temm. & Schleg.) and Chaenogobius annularius urotaenia (Hilgend.) and only at the latest time was indicated from the Amur basin on the gills of Siniperca chuatei (Bar.) by Ackmerov (1952) and by Gussew (1955). Besides,Ackmerov indicated that this species of Ancyrocephalus was described by him on Erythroculter oxycephalus (Bleck.), "apparently accidentally" which is undoubtedly a mistake in labeling. The finding of this species on Siniperca does not arouse any doubts in us after personal study of the material. Thus we must recognize as correct that A. mogurndae is encountered in three families of Perciformes, Electridae , Gobiidae and Serranidae. The first two are closely related to each other, whereas Serranidae are quite removed from them. It is possible that the conditions of existence in the fresh water help the transfer of A. mogurndae from the Bichok (Gobiidae Cottus sp., nobis) to Serranidae. One cannot fail to note one additional interesting circumstance and that is that in the Amur River, A. mogurndae is not encountered on Percottus glehni although this species is related to Eleotridae and it would seem would have all the chances to be infected, at any rate sooner than Sineperca.

Ancylodiscoides varicus is known from two very close species of Siluridae, and is indicated by Ackmerov from Liocassis ussuriensis (Dyb.) (Bagridae). As Gussew quite correctly points out (Gussew, 1955), the latter is undoubtedly erroneous.

Encotyllabe spari is encountered in Sparidae, Serranidae, and Pomadsyidae, i.e., on perciformids related to one superfamily, Percoidae, and undoubtedly related to each other.

In this same fashion Thaumatocotyle dasybatis is encountered in two genera of Trigonidae and on Rajidae; both families are undoubtedly related (Suvorov, 1948).

Heterocotyle minima is indicated on skates of two genera of Trigonidae and besides that on the shark--Squalus acanthias L. (Squalidae). There are no details whatsoever on the subject of the finding of H. minima on the latter species in the work of Price (Price, 1938a) in which this host is first cited. Thus, for the time being H. minima must be considered as being encountered only on relatively distant hosts, it is true apparently basically on skates and only accidentally on the shark.

Squalonchocotyle abbreviata has been discovered many times on Acanthias acanthias (L.) (Squalidae) and more rarely on Mustelus canis (Mitch.) (Carchahinidae). In addition to that, Palombi (Palombi, 1949) notes this species from Torpedo marmorata Risso on the basis of the data of Parona and Perugia (Parona and Perugia, 1890b). In connection with the last indication, one must suppose that it is faulty and actually refers to another species--Sq. torpedinis Price. Thus, the species under examination should be considered as encountered only on two closely related families.

Squalonchocotyle is apparently actually encountered on three species of three families of sharks, two of them are very close to each other--(Carchahinidae and Sphyrinidae) and one (Hexanchidae)--further removed from the first.

Three species of Monogenoidea occur on four species of fishes and are related to two genera of different families, but of one order: Heterobothrium affinis (Linton); Hexabothrium appendiculatum (Kuhn); and Gyrodactylus parvus Bychowsky.

Heterobothrium affinis is known with certainty from two species of Paralichthys (Bothidae) and from two species of Atherestes (Pleuronectidae). The consanguinous relations of these two families are obvious. In addition to that, the Paltus and Paltus-like flounders apparently are p. 233
closer to each other than other representatives of both families (Suvorov, 1948).

Hexabothrium appendiculatus is encountered on two species of Scyliorhinus (Scyliorhinidae) and two species of Mustelus (Carchahinidae). Both families of hosts are related to one suborder of Scyliorhinoidei (Berg, 1940) and have close consanguinous relations (Suvorov, 1948).

Gyrodactylus parvus is encountered in a number of representatives of the genus Nemachilus (Cobitidae) and in addition is indicated for Phoxinus brachyurus Berg (Cyprinidae). The latter is known from the works of Gvozdev and his collaborators (Gvozdev, Agapova, Martehov, 1953), who discovered this species in a rather considerable percentage of infection on the gills of Golyar (Phoxinus, nobis). Thus, G. parvus is undoubtedly encountered on representatives of two related families of fishes (see page 230), although its basic hosts are indisputably representatives of the genus Nemachilus.

Three species occur on three species of fishes related to two genera of different families of one order--Encotyllabe nordmanni Diesing, Trochopus tubiporus (Diesing), and Hexostoma thynni (Delaroche).

The first of these species was indicated from two species of *Brama* (Bramidae) and from *Heliastes chromis* (L.) Pomacentridae. Hence, we could not ascertain whence came the indications to the finding of *E. nordmanni* on *Heliastes* which was cited in the work of Price (Price, 1938a). In not a single one of the old resumés (Linstow, 1878, 1889; St. Remy, 1891-1892, 1898; Monticelli, 1907) is there mention of these data, and in the work of Price himself they are cited without any reference to the source. Thus, these data seem doubtful to us and is more likely that *E. nordmanni* must be considered as occurring only on Bramidae and that the indication to *Heliastes* is erroneous.

The second species--*Trochopus tubiporus*--is known from two species of *Trigla* (Triglidae) and indicated from *Cantharus lineatus* (Mont.) (Sparidae). The last host arouses certain doubts inasmuch as it is not even mentioned by Palombi in his resumé of Italian Monogenoidea (Palombi, 1949); however, one cannot say anything definite on this subject. Both families are related to one order but are very far from each other.

The third species--*Hexostoma thynni* is known from two species *Thunnus* (Thunnidae) and from *Sarda sarda* (Bloch.) (Cybiidae) but the close relations between those families has already been indicated (see page 230).

Thirteen species of monogenetic trematodes are encountered on two species of fishes of different genera related to different families of the same order, specifically: *Choricotyle charcoti* (Dollfus), *Ch. smaris* (Ijima), *Dactylogyrus inversus* Goto and Kikuchi, *Diplectanum aequans* (Wagener), *Encotyllabe pagrosomi* MacCallum, *Gyrodactylus medius* Kathariner, *G. fairporti* Van Cleave, *Microcotyle mouwoi* Ishii and Sawada, *Tetrancistrum sigani* Goto and Kikuchi, *Pseudaxine indicana* Chauhan, *Trochopus brauni* Mola, *Megalocotyle zschokkei* Mola and *Capsala martinieri* Bosc.

The question here about hosts of *Choricotyle charcoti* and *Ch. smaris* is complicated by the circumstance that these worms parasitize not only fishes themselves but also parasitic isopods (see page 431) which can transfer from one fish to another, carrying with them the *Choricotyle* which are present on them and by this fact confuse the true picture of the interrelations between the parasites and fishes. However, the existing data do not differ greatly from the majority of those which have already been discussed. Thus, *Ch. charcoti* is encountered on *Meinertia oestroides* Risso from *Trachurus trachurus* (L.) (Carangidae) and on the same isopod from *Box boops* (L.) (Sparidae); according to Berg both families of fishes are related to one superfamily Percoidae. *Ch. smaris* is encountered on p. 234
Cymothoa species from the buccal cavity of *Smaris vulgaris* Cuv. and Val. (Smaridae) and in addition apparently was discovered on *Meinertia oestroides* Risso (probably from *Box boops*) and on *Bopyrus squillarum* (Latr.) (host?) (he means the fish host of this isopod is unknown, *nobis*). Consanguinous relations between Smaridae and Sparidae are certain.

Dactylogyrus inversus is described from *Lateolabrax japonicus* (Cuv. and Val.) (Serranidae) and is often found on it, besides it is also indicated from the gills of the scombrid, *Pneumatophorous japonicus* Houtt. (Ishii and Sawada, 1938a). The latter seems unjustifiable to us and demands careful verification. Even though they are related to one order *Serranidae* and *Scombridae* are nevertheless very distant from each other.

Diplectanum aequans is described from *Morone labrax* (L.) and was encountered on it by a number of authors and is indicated from *Umbrina cirrhosa* (L.), the latter indication is made by Sonsino (Sonsino, 1890) and is undoubtedly erroneous because it refers to another species of *Diplectanum* as we succeeded in elucidating in our material (Bychowsky, 1957). Thus, up to this time, *D. aequans* has been encountered only on one species of host.

Similarly, *Encotyllabe pagrosomi* must be considered as occurring only on one species of fish--*Pagrosomus auratus* (Houtt.), because the indication of the finding of this species on *Caulolatilus* sp. actually refers to another species. Thus, Meserve (Meserve, 1938) described one sample of *Encotyllabe* under the name of *E. pagrosomi* and in the text indicated that this determination was provisional. Comparison between his data and the data of Price (Price, 1937b), although Meserve refers to the latter, indicates that the individual from *Caulolatilus* sp. must be considered as undetermined pending further findings, and at any rate it is not *E. pagrosomi*.

Gyrodactylus medius is described by Kathariner (Kathariner, 1894) from the gills of *Cyprinus carpio* (L.) (Cyprinidae) and from *Misgurnus fossilis* (L.) (Cobitidae) and then a mass of different *Gyrodactylus* from various fishes, but mainly Cyprinidae[1] was indicated under this name. There is no doubt that present knowledge gives basis with complete certainty to consider that this parasite is encountered only on *C. carpio* and that even Kathariner who described it was mistaken in thinking that *G. medius* was also encountered on *M. fossilis*[2]. Thus this species must be excluded from the group being examined and transferred into the group which has only one species of host. *Gyrodactylus fairporti* is indicated from *Cyprinus carpio* L. (Cyprinidae) and *Ameiurus melas* (Raf.) (Ameiuridae). This is undoubtedly a mistake and two different species are understood under one name and consequently *G. fairporti* actually must be considered as encountered on one species of host.

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[1] As is indicated in the text, *G. medius* is placed in the group under study on the basis of the fact that it was described from two species of fishes. It is understood that this is a provisional arrangement.

Microcotyle mouwoi is indicated by authors (a single finding) from *Siganus fuscescens* (Hout.) (Siganidae) and *Epinephelus chlorostigma* (Cuv. and Val.) (Serranidae). There are no commentaries whatsoever concerning the number of the findings in the work of Ishii and Sawada (Ishii and Sawada, 1938a). The fishes belong to different suborders of the perciformids which stand far from each other.

Tetrancistrum sigani is encountered by a number of authors on *Siganus fuscescens* (Hout.) and indicated by Ishii and Sawada on *Epinephelus chlorostigma* (Cuv. and Val.) in the same work where the preceding species is described. Just as it was about *Microcotyle mouwoi* nothing can be said about the relations of the host. Although this may never be substantiated, it seems to us that Ishii and Sawada were mistaken in determining the second species of fish and consequently their data are incorrect. p. 235

Pseudaxine indicana, described by Chauhan (Chauhan, 1945) from the gills of *Chrysophrys berda* (Forsk) (Sparidae), was later discovered by Manter (Manter and Prince, 1953) on an undetermined fish (local name, "salala") from Scombridae. Both families of hosts are quite removed from each other.

Trochopus brauni and *Megalocotyle zschokkei* were described by Mola (Mola, 1912) from the skin of *Cottus gobio* L. (Cottidae), but are undoubtedly parasites of other fishes belonging to the family Triglidae. The indication by the author of the species that he discovered the worms on fishes purchased in Rome and that they were present in the common basket with marine fishes, serves as a basis for such a conclusion. Just as all the other representatives of both genera are encountered only on marine fishes, it is more probable that here took

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[2] Incidentally, in describing *G. medius* Kathariner indicated *M. fossilis* as first (or primary, *nobis*) host, and *C. carpio*--the second. Thus, in the Russian literature the species which is taken for *G. medius* is not the species which should be so called because the species from *M. fossilis* should figure under this name. This question undoubtedly should be submitted to a special discussion, but it is not within the frame of the present work.

place an accidental transfer to *Cottus gobio*. It was further established that the first species is encountered on *Trigla hirundo* Bl., and the second was discovered on *Dactylopterus volitans* L. (Palombi, 1949). Thus both species must be placed in the species parasitizing one species of host each.

Finally *Capsala martinieri* was discovered on *Diodon* sp. (Diodontidae) and *Mola mola* (L.) (Molidae), i.e., on representatives of closely related families.

Thus, the second type of the group of monogenetic trematodes encountered on fishes of one order but of different families were analyzed. Of the 37 species indicated in the literature, the analysis forces us to exclude as incorrectly entered herein (in the group that parasitizes more than one species of fish, *nobis*) and encountered actually only on one species of fishes: *Diplectanum aequans* Wagener, *Encotyllabe pagrosomi* MacCallum, *Gyrodactylus medius* Kathariner, *Trochopus brauni* Mola, *Megalocotyle zschokkei* (Mola), *Axine belones* Abildgaard, and *Gyrodactylus fairporti* Van Cleave. It is probable that one must also exclude as erroneously indicated by the second type (genus, family) fishes (type of relationship of the hosts, *nobis*): *Dactylogyrus inversus* Goto and Kikuchi, *Microcotyle mouwoi* Ishii and Sawada, and *Tetrancistrum sigani* Goto and Kikuchi. Those three doubtful cases are based on the data of the same work by Ishii and Sawada but unfortunately cannot be verified. Similarly it is apparently necessary to exclude from the list of this group, *Amphibdella maccallumi* Johnston and Tiegs, *Ancylodiscoides varicus* Ackmerov, and *Encotyllabe nordmanni* Diesing as encountered only on one family of fishes. The remaining 24 species are broken up into those encountered; 1) on two closely related families of fishes--12 species; 2) on three closely related families of fishes--five species; 3) two closely related families and one distant from the first--one species [*Ancyrocephalus mogurndae* (Yamaguti)] ; 4) on relatively distant from each other, two-five families of fishes--six species [*Microcotyle pomacanthi* MacCallum *Ancyrocephalus manilensis* Tubangui, *Squalonchocotyle abbreviata* (Olsson), *Trochopus tubiporus* (Diesing), *Pseudaxine indicana* Chauhan and *Heterocotyle minima* (MacCallum)] .

Thus we see that the basic mass of the species of this group is encountered only on more or less related fishes although belonging to different families of one order.

We now pass to another group of species encountered in fishes p. 236
of different genera of one family, that is in some degree closely related to each other. This concerns a considerably larger number of species--97, that is almost twice as large as in both groups examined earlier. Of this number, 41% falls among representatives of the genus *Dactylogyrus*--40 species. During the study of this genus by us almost 20 years ago (Bychowsky, 1933a) we succeeded in showing that there is a regularity or

pattern in the distribution of separate species on their hosts. Specifically, the representatives of the genus Dactylogyrus basically are encountered on one species of host or on the species of one genus, and if on a second species of different genera, then the representatives of the latter (host genera) can cross-breed (hybridize, nobis). This conclusion, which was made on relatively small material, was later substantiated by more detailed observations. The proposed generalization was accepted by a number of researchers and is widely used in a number of theoretical works (Knorre, 1937; Ass, 1939; Rubtzov, 1940; Kirchenblat, 1941; Dogiel, 1947; Koratha, 1955a; and others). Very interesting data as well as the considerations of the subject are found in the work of Nybelin (Nybelin, 1936). Judging our work in 1933, he writes that in principle he agrees with the theory[1] proposed by Bychowsky and attempts to give it a certain theoretical basis. His considerations can be briefly summed up as follows. Since it is known that the infection of fishes takes place through the free-swimming larva, one must accept the fact that the searches for the corresponding hosts are based in a positive haemotaxis which apparently provokes albiginous (?, sic) substances specific for each species of fishes. For parasites which are encountered on only one host bear only one positively haemotaxic substance determined for each species of host, and for the ones encountered in two, three or more hosts, two, three or more "related" substances act on the larva. In the opinion of Nybelin this explanation refers not only to Monogenoidea but also to the miracidia of digenetic trematodes and also to all parasitic worms the larva of which actively seek their host. As will be apparent from what follows, these considerations of Nybelin coincide with ours in considerable measure (see page 289). Further, Nybelin establishes names for the forms which are enumerated on the one, two, three or many hosts. He proposes for them the terms, "monokapalisch," "di--", "tri--," "polykapalisch," corresponding to the number of the hosts on which the different species are encountered. These terms are hardly possible in the Russian language. Our "one--, two--, three-hosted, and so forth, parasites fully and distinctly replace the terms proposed by him. Nybelin quite truthfully underscores that for the studies on the subject of consanguinous relations of parasites and correspondingly their hosts, it is necessary to have a very precise classification of both. Unfortunately, he is also right saying that the old data are very often uncertain in this respect. As is seen from the above-mentioned this refers also to many contemporary materials in equal degree. Most interesting in the work of Nybelin are the data about his examination of the hybrids between separate

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[1] To call the proposed generalization, which mainly bears a private character a "theory" is at least an exaggeration; at best it deserves a name of a rule as it is accepted in Russian literature.

fishes. Thus he examined 7 samples of Rutilis rutilis x Abramis brama and in 5 cases discovered representatives of the genus Dactylogyrus, 8 samples of Scardinius erythropthalmus x Blicca bjöerkna on 4 of which appeared Dactylogyrus; three individuals of Abramis bram x Blicca p. 237
bjöerkna of which 2 were infected and finally one sample of Rutilis rutilis x Blicca bjöerkna on which there wasn't anything. The results obtained by him are presented in Table 5 composed by us. Nybelin thinks that because it is difficult to detect the identity of the parents of the hybrids the presentation of parasitological data for this would have been very interesting. He supposes that the finding of the parasites of one host on the hybrids would give sufficient basis to the establishment of one of the parasitic forms (parent species, nobis). Of all the one-hosted species encountered by him on the on the hybrids he considers Dactylogyrus crucifer, D. nanus, D. difformis, D. auriculatus, D. falcatus, D. cornu, and D. distinguendus, (as the only ones belonging to one host?, nobis). Evolving from this, he analyses his findings and comes to the conclusion about the possibility of utilizing Dactylogyrus for the determination of the parental forms of the hybrids. In addition to that, he considers that the findings of Dactylogyrus, which are peculiar to Abramis brama on Blicca bjoerkna are not correct and is the result of a mistake--a mistake for a Blicca bjoerkna of the hybrid individuals very similar to it which are actually mixtures between Abramis brama and Blicca bjoerkna. The analysis of Nybelin is undoubtedly interesting; however, as numerous researchers have shown, ours just as those of collaborators of our laboratory, he unfortunately was mistaken in the determination of one and many-hosted parasites, being carried away to excess in the direction of a very strict adaptability of one species to one species of host. Nevertheless, the general trend of Nybelin seems to us to be completely truthful and it seems fully justifiable to utilize peculiarities of the pattern of parasitism displayed by the species of Dactylogyrus for determining the parental forms of hybrid fishes. Thus for instance, the hybrid nature and p. 238
its origin in sample no. 8 in Table 5 is fully understood because of the composition of the species of Dactylogyrus encountered on it.

Coming back to the question concerning the occurrence of representatives of the genus Dactylogyrus on fishes forming hybrids, one must underscore that we are speaking here about viable hybrids, that is about those which underline close phylogenetic relations of the hybridizing fishes and which are related to different genera (Nikolukin, 1952). In other words, the ability to form hybrids is only an indication of the consanguinous relations of the host and the "rule" proposed by us can be formulated in a much simpler fashion--separate representatives of the genus Dactylogyrus are encountered either on one species of fishes or on several belonging to different but closely related genera, as is evident from the analysis which is conducted by us concerning the occurrence of species of monogenetic trematodes. This condition can, with different reservations which are, however, not numerous, be referred to all the Monogenoidea and in this fashion it represents a reflection of more general

TABLE 5

Infection by monogenetic trematodes of hybrid individuals of carp fishes (according to Nybelin, 1936)

No. II. II.	Host	Parasite	Number of parasitic individuals
1	*Rutilus rutilus* x *Abramis brama*	*Dactylogyrus crucifer* Wagener	2
2	Same	*D. crucifer* Wagener	1
		D. nanus Dogiel et Bychowsky	3
3	Same	*D. crucifer* Wagener	1
		D. fallax Wagener	6
4	Same	*D. crucifer* Wagener	10
		D. fallax Wagener	2
		D. suecicus Nybelin	1
5	Same	*D. fallax* Wagener	2
6	*Scardinius erytrophthalmus* x *Blicca bjoerkna*	*D. sphyrna* Linstow	1
7	Same	*D. fallax* Wagener	2
8.	Same	*D. sphyrna* Linstow	2
		D. distinguendus Nybelin	2
		D. cornu Linstow	1
		D. difformis Wagener	4
9	Same	*D. sphyrna* Linstow	7
		D. distinguendus Nybelin	1
		D. cornu Linstow	2
10	*Abramis brama* x *Blicca bjoerkna*	*D. wunderi* Bychowsky	1
11	Same	*D. auriculatus* (Nordmann)	1
		D. falcatus (Wedl.)	3
		D. sphyrna Linstow	1

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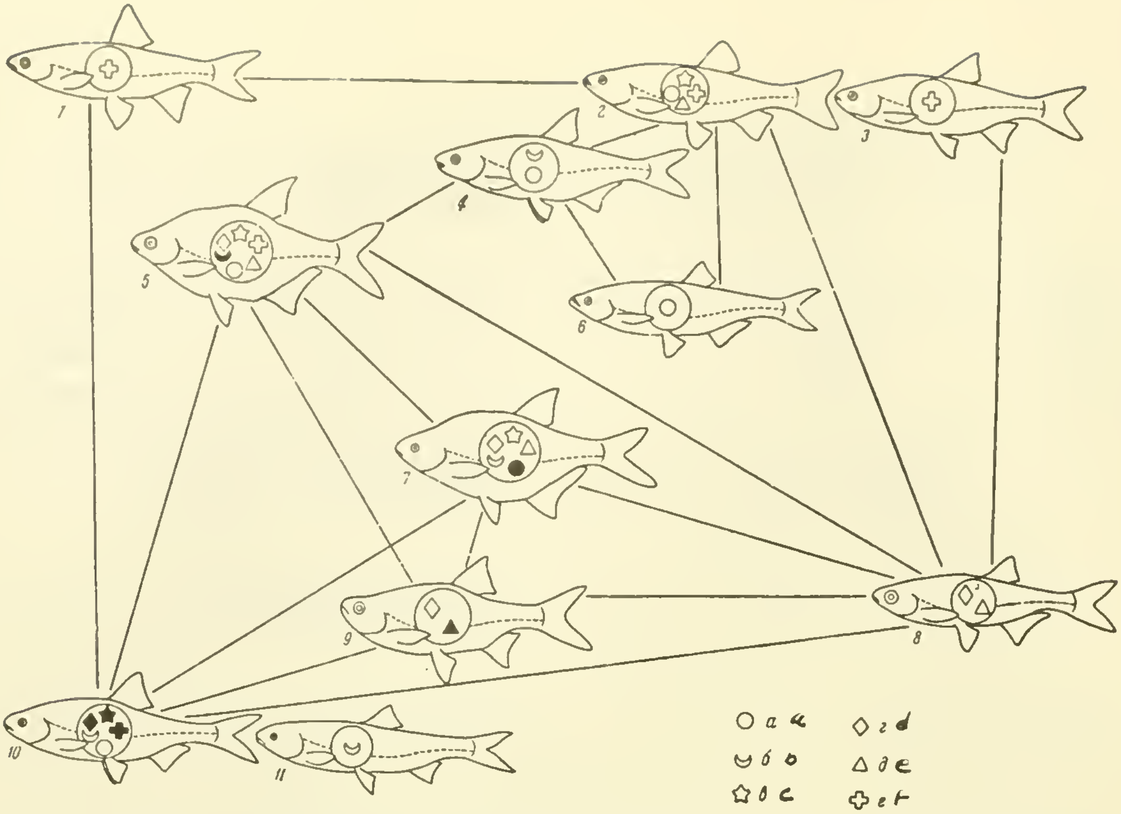

Fig. 261. Diagram of the distribution of certain species of Dactylogyrus on cyprinid fishes which hybridize among themselves. The lines between separate species of fishes indicate that these fishes hybridize with each other.
1--Chondrostoma nasus (L.); 2--Leuciscus cephalus (L.);
3--Leuciscus leuciscus (L.); 4--Vimba vimba (L.);
5--Blicca bjoerkna (L.); 6--Chalcalburnus chalcoides (Guld.);
7--Abramis brama (L.); 8--Alburnus alburnus (L.);
9--Scardinius erythrophthalmus (L.); 10--Rutilus rutilus (L.);
11--Rutilus frisii (Nordm.).
a--Dactylogyrus sphyrna Linstow; b--D. cornu Linstow;
c--D. nanus Dogiel et Bychowsky; d--D. crucifer Wagener;
e--D. difformis Wagener; f--D. similis Wagener. The symbols of species of parasite filled with black color indicate that the parasite is predominantely encountered in that particular fish.

normalities (rules, norms, principles, see other interpretations on page 220, nobis) which will be discussed later. However, taking into consideration the wide ability for hybridization among Cyprinidae, which appear to be the main hosts of Dactylogyrus, one cannot fail to recognize the necessity of preserving this "rule" because in its initial form it can be useful in some measure for the ichthyologists in their works on hybrid-type fishes and for parasitologists during their evaluation of peculiarities of infection of a determined circle of hosts within a particular region. As a matter of fact, these questions extend beyond the limits of the problems which interest us at the present time. Let us pass again to the factual material. Of the 40 species of Dactylogyrus encountered on two or more genera of one family of fishes, 30 are discovered on fishes of two genera (24 species on two species; four--on three; and two species on four species of fishes), two species each on three species of three genera of fishes and finally eight species of Dactylogyrus each on a number of fishes belonging to four or more genera. Of the 24 species found on two species of fishes of different genera, ten are encountered on fishes which produce hybrids [Dactylogyrus crassus Kulwiec, D. falcatus Diesing, D. alatus Linstow, D. haplogonus Bychowsky, D. parvus Wagener, D. wunderi Bychowsky, D. zandti Bychowsky, D. grislaginis Alarotu, D. gracilinneinatus Alarotu, D. acus (Mueller)]. 12 on fishes of genera very close to each other which were not differentiated until recently (D. acutatus Mueller, D. gussevi Achmerov, D. navicularis Gussew, D. gobioninum Gussew, D. markewitschi Gussew, D. facetus Gussew, D. tendibulus Gussew, D. rimsky-korsakowi Gussew, D. curvicirrus Achmerov, D. parabramis Achmerow, D. palliatus Gussew, D. vancleavi Monaco and Mizelle), and only the finding of two species causes certain perplexity. The first of them is D. megastoma Wagener--it is indicated in the literature on Rhodeus sericeus (Pall.) and Blicca bjöerkna (L.). The considerable separation of these hosts forced us to doubt the correctness of these data. During their verification it was clarified that in the first place D. megastoma was found only by the author of this species and wasn't discovered by anyone after him, and in the second place that the indication of its presence on Blicca bjöerkna is based on the legend to the figure of the egg of D. megastoma from the gills of Blicca bjöerkna (Wagener, 1857a, page 109). In conclusion one can consider with large measure of probability that the given species is encountered only on one host--Rhodeus sericeus.

The second species--D. ramulosus Malewitskaja--is known from numerous findings on the gills of Leuciscis idus (L.) and is indicated from Rutilis rutilis (L.) from the single finding of several samples of p. 240
worms on one sample of fish from the middle-flowing (mid-stream?, nobis) of the river Tissa (Zakhvatkin, 1951). The latter indication undoubtedly is erroneous and is based on an incorrect determination either of the host or the parasite. We do not doubt this because many times during the verification of preparations by V. A. Zakhvatkin we became convinced of the inaccuracies of his determinations. Thus, both species of Dactylogyrus

which cause doubt apparently are encountered only on one host. Of the four species of Dactylogyrus indicated for three fishes of two genera, two live on fishes among whom hybrids are known (D. vastator Nybelin, and D. anchoratus Dujardin), 1--(D. robustus Malewitskaja) on two vicarious (representative?, nobis) species, Leuciscus sp. and on Aspius aspius which hybridize with one of the preceding species. Finally the last species--D. drjagini Bychowsky--is encountered on fishes of two genera close to each other among whom hybrids are still unknown but very probable. Two species encountered on four species of fishes of two genera (D. linstowi Bychowsky and D. tuba Linstow) have fishes which hybridize as hosts.

D. minor Wagener and D. fraternus Wagener are encountered on three species of fishes of three different genera and one of the hosts of the first hybridizes with the two others, whereas the hosts of the second all hybridize with each other.

Most interesting are the last eight species of Dactylogyrus encountered on a large number of hosts relating to four or five genera, specifically: D. nanus Dogiel and Bychowsky, D. similis Wagener, D. sphyrna Linstow, D. cornu Linstow, D. crucifer Wagener, D. difformis Wagener, D. fallax Wagener, and D. magnichamatus Achmerov. The relations between the hosts of six species to each other and their ability to hybridize and the character of the Dactylogyrus occurring on them is indicated in figure 261. Hence, it is obvious that, with the exception of D. nanus, the classification of all species strictly corresponds to the data based on the presence of hybrids between the corresponding hosts. As regards D. nanus, its finding on Leuciscus cephalus (L.) will fit into the scheme if it is discovered on Vimba vimba (L.) or on Chondrostoma nasus (L.) or Alburnus alburnus (L.), which seems very probable to us. From the same scheme it is apparent that in all probability the same species must be discovered on Alburnus alburnus (L.) and Leuciscus leuciscus (L.). This is also substantiated by the fact that there are common species on Leuciscus cephalus and Alburnus alburnus, for instance D. parvus Wagener.

Dactylogyrus fallax Wagener is indicated erroneously in a number of fishes in our work which was written during our student days (Bychowsky, 1929). Actually, the hosts of D. fallax are related to the genera of Abramis, Blicca, Rutilus, Leuciscus, and all form hybrids.

D. magnichamatus Achmerov is encountered on six species: Hypophthalmichthys molitrix (Val.), Erythroculter erythropterus (Bas.) Er. mongolicus (Bas.), Culter alburnus Bas., Hemiculter leucisculus (Bas.), and Megalobrama terminalis (Rich.). At first, one specimen of this species was discovered on the first species of host, and described from it by A. H. Achmerov in 1952. Subsequently it was discovered by A. V. Gussew on all the rest of the hosts, but he never once found it on

Hypophthalmichthys (Gussew, 1955). All the five species on which *D. magnichamatus* was found by Gussew belong to one subfamily--Cultrinae and thus are related in a certain degree to each other, whereas which Achmerov described this species belongs to the subfamily of Hypophthalmichthyinae, generally distant from Cultrinae. It is difficult to say anything definite until new studies, but it seems to us that the data of p. 241 Achmerov demand very thorough verification. It is possible that here there was some error in labeling. All in all this is the only case from the genus *Dactylogyrus* which does not fit into the "rule of Bychowsky."

Among the species of other genera of Monogenoidea related to the groups encountered on two or more genera related to one family of fishes,. an overwhelming majority is discovered in representatives of more or less closely related genera. Among the species of this group a few cause perplexity and because of that we must deal primarily with them and also with several others which deserve attention for different reasons. First of all one must discuss the occurrence of certain representatives of the genus *Diclidophora*. Thus, *D. denticulata* Ollson and *D. maccallumi* (Price) are indicated as discovered on Gadidae belonging to different subfamilies and *D. pollachii* (Beneden and Hesse), *D. minor* (Ollson) and *D. morhuae* (Beneden and Hesse) which are on genera that are quite distant from each other even though they are of one subfamily. During more careful re-examination it appears, however, that all these worms apparently occur each only on one species of hosts and the indications (that they occur, *nobis*) on the others are faulty or erroneous.

Thus, *D. denticulata* is indicated from *Merluccius merluccius* (L.) on the basis of the data of Baylis and Jones (Baylis and Jones, 1933) who found this species on the given fish in Plymouth. However, as Sproston quite correctly notes (Sproston, 1946) these data are based on an erroneous determination of the host "because of the superficial similarity of *M. merluccius* to *Gadus* (=*Pollachius*) *virens*--a mistake often made by non-ichthyologists." This is substantiated by the fact that in the region of Plymouth, *D. denticulata* is very common on the Pollack, whereas it has never since been discovered by anyone on *M. merluccius*.

The case of the finding of *D. denticulata* on *Trisopterus minutus* (Müll.) is not clear--there is only one indication of Parona (Parona, 1899, 1902) about the given host. Probably there is some mistake. Thus the authentic host of *D. denticulata* is only one species--*Pollachius virens* (L.) on which this worm is encountered rather frequently practically throughout its entire range.

D. maccallumi was described in Price (Price, 1943a) only from one species, *Urophycus chuss* (Wall.); whereas the indication of its finding on *Merluccius bilineatus* (Mitch.) which was not taken into consideration by Price and cited anew, completely uselessly, by Sproston in her resumé is based on the earlier data of MacCallum (MacCallum, 1917). Thus, even the given species actually is encountered only on one host.

D. pollachii and D. minor are indicated as discovered on Odontogadus merlangus (L.), the first in addition on Pollachius pollachius (L.) and the second on Micromesistius poutassou Risso, and the usual host for both species is the second host. The data about the finding of D. pollachii on Odontogadus belong mainly to the first half and middle of the last century and are apparently based on a faulty determination of the parasite. Indications to the presence of D. minor on Odontogadus are found only in one work (Rees and Llewellyn, 1941) and as Sproston correctly writes, "if the identifications of host and parasite are correct, this is one of the exceptional departures from rigid host-specificity in the subfamily." (Sproston, 1946, page 482). It is more probable that here takes place an error in determination.

Finally, the data about the finding of D. morrhuae on Odontogadus merlangus (L.) in addition to the usual host, Gadus morrhua (L.), are based on the inaccurate determination of the parasite and refer to another species p. 242
as Price correctly points out (Price, 1943a).

From the seven species of Urocleidus pertaining to the given group (this group of parasites under consideration, nobis), U. mucronatus Mizelle[1] encountered on Helioperca incisor (C. and V.), Allotis humilis (Giz.), Eupomotis gibbosus (L.) and Lepomis macrochirus Raf. deserves special mention. All the enumerated species are very close to each other; this is substantiated on the one hand by the fact that they have often been transferred from one genus into another (thus H. incisor was formerly referred to the genus Pomotis and to Lepomis, Allotis humilis--to the genus Lepomis, etc.), and on the otner that these species hybridize. It is interesting that the proximity of the enumerated hosts is substantiated by the finding of U. mucronatus on the hybrids between H. incisor and E. gibbosus and between A. humilis and E. gibbosus (Mizelle, 1936).

Among eight species of Gyrodactylus related (to this group of parasites under consideration, nobis) one must note two species--G. groenlandicus Levinsen and G. gobioninum Gussew. The first of these is described by Levinsen (Levinsen, 1881) from Myoxocephalus scorpius (L.) and then encountered by us in the Pacific Ocean near the shores of Sakhalin and near the southern Kurile Islands on young Myoxocephalus species, Blepsias cirrhosus Jord. and St. and Opisthocentrus zonope

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[1] There is reason to believe that this species is a synonym of U. ferox Mueller, 1934 (Mizelle and Donahue, 1944).

Jord. and Sn., and the individuals from the Far Eastern fishes were placed by us into a special subspecies *G. g. pacificus* Bychowsky and Poljanski (Bychowsky and Poljanski, 1953). All the hosts are related to Cottidae, but are nevertheless distant from each other. The impression is created that in addition to the consanguinity, contemporary ecological factors also play a role here--*G. groenlandicus* infests fish living on the littoral whereas the individuals of the same fishes which inhabit depths remain free from this parasite. As a matter of fact, we have already spoken about certain ecological influences on infection in the chapter about life cycles and, in addition, this question will be studied specially later (page 286).

G. gobioninum was recently described by A. V. Gussew from fishes related to six genera, *Hemibarbus*, *Pseudoraspora*, *Chilogobio*, *Sarcochilichthys*, *Pseudogobio*, and *Saurogobio*. According to Kruzhanovsky (1947) all these genera are related to Gobioninae (Gobiini, *nobis*) whereas according to Berg the first genus belongs to Barbini and the rest to Gobiini (Berg, 1912). At any rate the hosts of *G. gobioninus* are rather removed from each other and judging from the morphological data, this species apparently is cumulative (lumped from a number of species that should be separated, *nobis*) as Gussew noted and described it (1955). Thus it is more probable that the "forms" from different hosts appear to be independent; in any case, this applies to the one parasitizing *Hemibarbus*.

The last species of this group which we consider necessary to discuss is *Mazocraes harengi* (Beneden and Hesse) indicated for *Clupea harengus* L. and *Alosa alosa* L., fishes related to different subfamilies (Svetovidov, 1952). Because *Cl. harengus* is the typical host of *M. harengi* the correctness of the data about the finding of this parasite on *A. alosa* is subject to doubt. As far as we know the indication on the last host exists only in the work of Baylis and Jones (Baylis and Jones, 1933). During the evaluation of this work, it appears that actually *M. harengi* is indicated for *Clupea* (=*Alosa*) *alosa* first according to the data of "the junior author" (Jones). Until there are sufficiently documented subsequent findings, we have no basis for taking these data into account. It is more probable that the "junior author" is simply mistaken in the determination and was dealing p. 243
with *Mazocraes alosae* which, it must be mentioned, he was finding on *Alosa finta*. The numerous studies on the herrings which were conducted from 1933 which indicate the absence of *M. harengi* on representatives of the genus *Alosa* can serve as substantiation for this.

All in all, one can consider that the degree of proximity of the hosts of Monogenoidea which are encountered among fishes of different genera of one family is not characterized only by belonging to the latter but it is considerably larger and the worms are usually encountered on the genera closer to each other than to genera of a given family as a whole.

In cases of finding monogenetic trematodes on more distant genera of the hosts, it appears during their verification that this is either a result of some mistake in the determination of the host or the parasite, or the species of the parasite is represented by certain lowest taxonomic units (subspp. ?, *nobis*),the occurrence of which is characteristic only for a certain genus of hosts but not for all, which is analogous to what we saw earlier in *Gyrodactylus arcuatus* (page 223).

We shall summarize certain results without stopping to analyze the species encountered on representatives of a single genus because there are no doubts whatsoever that these species of hosts basically are phylogenetically very close to each other.[1]

As the preceding analysis has shown more or less accurately, only 32 species or 3.3% of the total number of the previously examined monogenetic trematodes are encountered on fishes of different families of one or several orders. However, during the verification of the occurrence of these species we succeeded in showing that the great majority of them is found on fishes which have to a certain degree, consanguine links with each other, and in this fashion do not represent special exceptions to the general rule about the occurrence of the species of monogenetic trematodes on consanguinous fishes--a rule which undoubtedly emerged (is the logical outcome, *nobis*) from everything that has gone before. Only nine species do not fit into this rule of which (*Calicotyle affinis* Scott and *Gyrodactylus arcuatus* Bychowsky) are encountered on fishes of two different, unrelated orders and seven [*Ancyrocephalus manilensis* Tubangui, *A. mogurndae* (Yamaguti), *Trochopus tubiporus* (Diesing), *Heterocotyle minima* (MacCallum), *Squalonchocotyle abbreviata* (Olsson), *Pseudaxine indicana* Chauhan and, *Microcotyle pomacanthi* MacCallum] occur on several families of one order of fishes which are only slightly related. If we should examine once more the data on the finding of these nine species, we could express certain supplementary doubts about the correctness of placing six of these species in the given group. Thus, even though it is encountered on fishes of different orders, *G. arcuatus* forms special subspecies which are characteristic only for the fishes of the determined order and even more--of the genus (species) of fishes. For that reason this case can be interpreted differently, but at any rate it would be more correct to judge the occurrence of subspecies and not of the species as a whole, especially since they could be considered species (which are, *nobis*) close to each other. If we accept this, then the subspecies of *G. arcuatus* do not form any exception from the general rule. As has already been pointed out, *A. manilensis* is apparently encountered in artificial conditions p. 244 and not in nature, hence, it is difficult to speak about its natural occurrence. It is possible that here takes place infection of unusual hosts similar to the one which we have seen from *Benedenia melleni* (MacCallum). We cannot fail to note that all the families of the hosts of this species are related in some (true, farther removed) degree. As has already been pointed out, the data about *Trochopus tubiporus* and *Squalonchocotyle abbreviata* provoke great doubts and probably in both cases there must be a mistake. It is possible that *Heterocotyle minima* actually is encountered only on Trigonidae and the indication of its finding on the shark is erroneous; until the data of Price are substantiated it is difficult to solve this problem either way convincingly. Finally, the data of MacCallum on *Microcotyle pomacanthi* demand verification (as do the majority of his data on occurrence). If one should consider that the indication of the finding of this species on Labridae is faulty, then the remaining four families are close to each other as we indicated. As a result, the data about the six species enumerated before cause doubts to some degree and demand further substantiation and re-examinations. Thus, only *Calicotyle affinis*, *Pseudaxine indicana*, and *Ancyrocephalus mogurndae* are fully authenticated as occurring on unrelated species, that is, all in all, 0.3% of the total number of the Monogenoidea.

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[1] In the work which was cited by us in 1933 we examined a special case where the degree of parentage of the hosts related to one genus of *Abramis* arouses certain doubts. To summarize, the analysis of the occurrence of the species of *Dactylogyrus* peculiar to the separate species of fishes shows that it is possible that the species of the genus *Abramis* should be placed in three different genera. During subsequent works, however, new data were received about the occurrence of *D. auriculatus* Nordm. on *A. ballerus* which indicated that the Cinets (*A. ballerus*, *nobis*) is possibly closer to the Shch (*A.* sp. *nobis*) than the Beloglazka (*A. sepa* , *nobis*).

We examined the question about the occurrence of species of p. 245 monogenetic trematodes on their hosts without taking into account the quantitative side of the question, i.e., without taking into consideration the frequency of occurrence of any given species of parasite on any given species of fishes, but nevertheless, the corresponding data substantiate the established normalities (generalities or principles, see above, *nobis*) (certain materials on this subject can be found in the preceding text.). One can consider that in the case of the occurrence of any species on a number of hosts, it is encountered, as a rule, in a considerably greater percentage on one of them and the number of individual parasites on this species of the host is more numerous than on all the others. This can be illustrated by the following table based on our data with . V. A. Dogiel and those of A. P. Markevich (Table 6). From it we see that the percentage of infection and the number of parasites in one "basic" host is immeasurably larger than among others--the "secondary" host. Similarly the same can be seen from the data of Hargis (Hargis, 1953) concerning the occurrence of certain American monogenetic trematodes (Table 7).

TABLE 6

Occurrence of certain Dactylogyrus on their Hosts
(according to data of V. A. Dogiel and B. E. Bychowsky 1938--
Delta of the Volga, and A. P. Markevich, 1949--Dniepr, near Kanev)

Parasite	Region of Research	HOST					
		Rutilus rutilus		Blicci bjöerkna		Abramis brama	
		Delta of the Volga	Dniepr near Kanev	Delta of the Volga	Dniepr near Kanev	Delta of the Volga	Dniepr near Kanev
Dactylogyrus crucifer Wagener	% of infection	100.0	100.0	8.0	4.0	3.3	0
	number of parasitic individuals on fish						
	samples	75-80	6-167	6-12	9	1	0
Dactylogyrus nanus Dogiel et Bychowsky	% of infection	30.9	28.0	4.0	8.0	3.3	4.0
	number of parasitic individuals on fish						
	samples	1-15	1-11	25	1-8	4	1
Dactylogyrus cornu Linstow	% of infection	2.4	0	40.0	24.0	0	8.0
	number of parasitic individuals on fish						
	samples	10	0	2.100	1-47	0	2-5
Dactylogyrus sphyrna Linstow	% of infection	7.1	8.0	40.0	20.0	0	4.0
	number of parasitic individuals on fish						
	samples	1-3	1-6	2-22	2-9	0	2
Dactylogyrus zandti Bychowsky	% of infection	--	--	4.0	4.0	33.3	16.0
	number of parasitic individuals on fish						
	samples	--	--	8	3	50-60	4-37

TABLE 7

Occurrence of certain American Monogenoidea
(according to Hargis, 1953)

Parasite	HOST Chaenobryttus coronarius (Bartran)	 Eupomotis gibbosus (L.)	 Lepomis macrochirus (Raf.)
	Number of parasites found		
Actinocleidus fergusoni Mizelle	1	-	546
Cleidodiscus robustus Mueller	1	64	-
Urocleidus dispar (Mueller)	11	186	171
Urocleidus chaenobryttus Mizelle	253	-	3[1]
Urocleidus ferox Mueller	1	515	1148
Number of openings	18	7	34

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[1] This, apparently, is an error.

However, the above-mentioned "rule" appears to be too general and insufficiently precise. Already from Table 7 we see that Urocleidus dispar is encountered almost in equal quantities both among Eupomotis gibbosus and among Lepomis macrochirus, fishes closely related to each other which are placed by many into one genus Lepomis (actually, in the work of Hargis E. gibbosus is placed in the genus Lepomis), whereas in the relatively distant species Chaenobryttus it is encountered in very small numbers. Close relations are apparent also among U. ferox, the main host of which nevertheless is Lepomis macrochirus. Similar cases are not rare where there are two "basic" hosts for a determined species of monogenetic trematode. This we see in Dactylogyrus vastator Nybelin which occurs almost in the same percentage on the Carp (Cyprinus carpio, nobis) and Karas (Carassius sp. nobis), in D. tuba Linstow on the Yaz (Leucisus idus, nobis) and Zhereh (Aspius aspius, nobis), in Tetraonchus monenteron (Wagener) parasitizing Esox lucius L. and E. reicherti Dyb., etc. In addition to that, in separate cases we encounter a large number of "basic" hosts but it is not possible to say which one of them is "the p. 246 most basic." Herrings of the genus Alosa for Mazocraes alosae could serve as a sample of such "basic" hosts. Thus, in the Caspian Sea this monogenetic trematode is encountered on A. kessleri (Grimm) in 80-100%, on A. brashnikowi (Borodin) in 70-100%, on A. saposhnikovi (Grimm) in 100%, and on A. caspia (Eichwald) in 40-92% which is approximately the same frequency on all four types. As a rule the presence of two or more basic hosts shows that the latter are considerably closer to each other than to other hosts. For instance, Diclybothrium armatum Leuckart infects all the representatives of the genus Acipenser of the Delta of the Volga in almost the same way and is seldom encountered on Huso huso (L.). We did not find this species even once on the last host (Dogiel and Bychowsky, 1938), and Ivanov and Muregin (1936) found it only once. As an example of such relations, Ancyrocephalus paradoxum Creplin parasitizes, in more or less the same high percentage, on Psudak (Lucioperca sp. nobis) and little Berch [Lucioperca volgensis (Gmelin)] which is encountered relatively seldom on the Okoun (Perca sp. nobis) and is never encountered on the marine Psudak (L. marina Cuv.). Without dealing with this question any further we can accept wholly that with the occurrence of the species of monogenetic trematodes on a number of species of fishes of one or several genera, families, or even orders., it is encountered on one or several closely related ones in a larger percentage and for the most part in greater numbers than on others which are far removed phylogenetically: On the average, the percentage of infection of the latter decreases in proportion to the separation from the basic host. It is understandable that this normality depends to a great extent on concrete geographical and ecological conditions in which the given species is located. Thus, the degree of infection of the Okoun (Perca sp., nobis) by Ancyrocephalus paradoxus Creplin which was discussed previously depends upon the conditions of the body of water in which they live and particularly whether or not the Psudak (L. sp., nobis) are present there and what is the numerical population of the Okoun.

In speaking about "basic" and "secondary" host, it is indispensable to note that the "basic" host is not equivalent to the host which is historically initial (first, nobis); this can be, as we shall try to show, observed in a majority of the cases, but it is not essential because the meaning of "basic" host is related to concrete conditions of the contemporary slice of time and the initial host actually may not be the most favorable but the host which was infected relatively recently. Inasmuch as we judge which is the "basic" host according to the quantitative indices this is fully understandable. As an example which confirms these considerations can be cited the data on Nitzschia sturionis Abildgaard in the Aral Sea. If we judge by the number (quantity, nobis) of infections, then it is understandable that Acipenser nudiventris Lev. appears to be the basic host of the parasite. However, we know that historically this species of fishes is the new host for N. sturionis in the given body of water for they (the fish, nobis) were infected by them (N. sturionis, nobis) only in the 1930's during the transfer of the infected Stellated Sturgeon into the Aral Sea from the Caspian (Lutta, 1937; Dogiel, 1947). The data about Gyrodactylus nemachili Bychowsky can serve as another equally interesting example. This species was discovered in the basin of the river Ili on eight species of fishes (and on one accidentally), namely: Nemachilis strauchi (Kessl.) in 20% of fishes, with an intensity of from 1-15 individuals per fish N. labiatus (Kessl.) (14. 3%; 2-6 individuals on the fish), N. dorsalis (Kessl.) (29. 0%; 1-20 individuals on the fish), N. stoliczkai (Steind.) (6. 6%; 1-4 individuals on the fish), N. sewerzowi G. Nik. (25. 0%; 1-3 individuals on the fish). Phoxinus brachiurus Berg (61. 8%; 1-15 individuals in the fish), Schizothorax pseudaksaiensis Herz. (11. 1% equals one case and 1 specimen) and Sch. argentatus Kessl (3. 3% p. 247
equals one case and one specimen) (Gvozdev, Agapova and Martehov, 1953). Phoxinus brachiurus with its considerable infection appears to be the basic host; however, there is no doubt that historically, representatives of the genus Nemachilus are the most initial (primitive, nobis) hosts as is proven by the morphological peculiarities of G. nemachili similar to those among other species of Gyrodactylus from Cobitidae. However, the given example demands careful analysis from the point of view of correlation of the existing information about the relations of the hosts to each other in connection with the above-mentioned rule. First of all we must note what is known about the presence of hybrids between representatives of the genus Phoxinus and Nemachilus (see Berg, 1912, page 10). Thus, the finding of D. nemachili on both of these genera corresponds to the rule which was proposed by us for Dactylogyrus. The finding of G. nemachili on both species of Schizothorax is extremely rare and its intensity is minimal, which corresponds to the above-mentioned rule about the frequency of occurrence on the moredistant "secondary" hosts which both species of Schizothorax represent.

The infection of five species of Nemachilus is of the greatest interest. If we arrange them according to the percentage of infection and intensity of invasion, we obtain the following list (from the stronger to the weaker infection); N. dorsalis, ? N. sewerzowi, N. strauchi, N. labiatus, *N. stoliczkai,* and ? *N. sewerzowi.* *N. sewerzowi* occupies a more or less undetermined place in this list. It has a high percentage but low intensity of infection, and it is for this reason that it is indicated with a question mark in two places. If we turn to the ichthyological data, we shall see that *N. dorsalis, N. strauchi* and *N. labiatus* belong to the subgenus *Deuterophysae,* the remaining two species to the subgenus *Nemachilus* (s. str.). Within the limits of the first subgenus, *N. dorsalis* and *N. strauchi* are closer to each other and the latter in its turn is close to *N. labiatus.* The following data serves as a basis for this. *N. strauchi* and *N. dorsalis* apparently form hybrids among themselves; in any case a subspecies *N. strauchi dorsaloides* intermediary between *N. strauchi ulacholicus* and *N. dorsalis* is described from the region of Issik-Kulya (Turdakov, 1947). On the other hand two variations which apparently represent hybrids of this species with *N. strauchi* are known for *N. labiatus* (Berg, 1949, page 857). Thus, according to the degree of consanguinity the examined fishes can be arranged as follows: *N. dorsalis*--*N. strauchi*--*N. labiatus*--*N. stoliczkai,* which as we see fully corresponds to the list composed in accordance with the nature of infection by *G. nemachili.* The question about the status of *N. swerzowi* remains unclear. Obviously, it must be solved by ichthyologists, but taking into consideration the data on *G. nemachili* and the fact that the swim bladder of this fish has a free part and also that it is small and resembles the one among representatives of the subgenus *Deuterophysa* (see Berg, 1949, page 851), it seems probable to us that this species is placed erroneously in the subgenus *Nemachilus* s. str. and that it stands closer to *Deuterophysa.* If this is substantiated then its high percentage of infection and at the same time its low degree of intensity will become fully understandable. All in all, we notice almost complete coincidence of the data on phylogenetic relations of fishes with the character of infection of the "basic" and "secondary" hosts.

As a result of the examination of the entire material on occurrence of speciès of monogenetic trematodes on the species and genera of fishes, one can consider as fully established the following:

1. A great majority of species of monogenetic trematodes is encountered only on one species or representatives of one genus of fishes. p. 248

2. When monogenetic trematodes are encountered in several genera of fishes, the latter stand in phylogenetic relations and, in an overwhelming majority of the cases, are related to one family.

3. The finding of species of monogenetic trematodes on the representatives of different families of one or several orders of fishes occurs rarely and in these cases one can show that consanguinous links exist between the hosts.

Only three cases are authentic exceptions to the above-mentioned rules--the distribution on their hosts of Pseudaxine indicana Chauhan, Calicotyle affinis Scott, and Ancyrocephalus mogurndae (Yamaguti). However, we shall attempt to show later that even the two last species are not just simple exceptions to the general rule.

CHAPTER III

OCCURRENCE OF THE GENERA OF MONOGENETIC TREMATODES ON FAMILIES AND ORDERS OF THEIR HOSTS--FISHES

There is no doubt that the materials presented above demand p. 249
further examination; however, before passing to it we must turn our attention to the following group of facts, namely--to the nature of occurrence of the genera of Monogenoidea on the families of fishes. Just as in the preceding presentation which was dedicated to the discussion of the summary Table 4, we shall utilize the materials on the same 958 species and examine the data obtained one by one starting from the genera encountered only on one family of fishes. In the first place, in the discussion about occurrence we will have to utilize the corrections which were made earlier, and in the second place conduct a certain verification of the initial materials which demand significant changes in a number of cases as will be seen later. Speaking about utilization of the previous data we mean that in the text and tables that will follow, faulty or doubtful data which have already been analyzed before will not be included; specifically,that for a number of genera the data about the finding on separate families of hosts will be excluded: *Amphibdella* [*A. maccallumi* (Johnson and Tiegs)] on Squalidae; *Bilaterocotyle* [*B. chirocentrosus* (Chauhan)] on Chirocentridae; *Cyclocotyla* (*C. bellones* Otto) on Sparidae and Maenidae; *Dactylogyrus* (*D. inversus* Goto and Kikuchi) on Scombridae; *Diclidophora* [*D. palmata* (Leuckart)] on Bothidae; *Calicotyle* (*C. kroyeri* Diesing) on Bothidae; *Encotyllabe* (*E. nordmanni* Diesing and *E. pagrosomi* MacCallum) on Pomacentridae and Latilidae; *Heterocotyle* *H. minima* (MacCallum)] on Squalidae; *Megalocotyle* [*M. zschokkei* (Mola)] on Cottidae; *Squamodiscus* (*S. belengeri* Chauhan) on Muraenidae; *Tetrancistrum* (*T. sigani* Goto and Kikuchi) on Serranidae; *Trochopus* (*Tr. brauni* Mola) on Cottidae; and, *Urocleidus* (*U. mimus* Mueller) on Esocidae. In addition, during the tabulation of the number of species parasitizing a given family the indications for *Gyrodactylus* on the presence of *G. medius* Kathariner on Cobitidae and for *Diplectanum* on *D. aequans* (Wagener) from Sciaenidae will be excluded. Further,for *Ancyrocephalus*--(*A. alatus* Chauhan) information about the finding on Ariidae, Mugilidae, and Scopelidae and for *Diplectanotrema* [*D. balistes* (MacCallum)] all the data about the families of hosts are given with a question mark even though they are preserved in the tables. Finally,in addition to those indicated for *Benedenia* [*B. melleni* (MacCallum)] information about the findings only in natural conditions will be included in the table.

Among the 154 known genera of monogenetic trematodes of fishes, 95, i.e., almost two-thirds, are encountered each only on one family of fishes. Of these genera, 67 contain only one known species at p. 250

TABLE 8

Monotypic genera of Monogenoidea, parasitizing one family of fishes.

Genera	Families of fishes
1. Allopseudaxine	Thunnidae
2. Allodiscocotyle	Carangidae
3. Ancyrocephaloides	Triacanthidae
4. Anonchohaptor	Catostomidae
5. Anoplocotyle	Sparidae
6. Anthocotyle	Gadidae
7. Anoplodiscus	Sparidae
8. Bychowskyella	Bagridae
9. Bothitrema	Bothidae
10. Bicotylophora	Carangidae
11. Bilaterocotyle	Sciaenidae
12. Callorhynchicola	Callorhynchidae
13. Calceostomella	Sciaenidae
14. Chimaericola	Chimaeridae
15. Chauhanea	Sphyraenidae
16. Dermophthirius	Carcharhinidae
17. Dasybatotrema	Trigonidae
18. Dictyocotyle	Rajidae
19. Diplasiocotyle	Mugilidae
20. Diplectanocotyle	Megalopsidae
21. Empleurosoma	Serranidae
22. Enoplocotyle	Muraenidae
23. Empruthotrema	Rajidae
24. Faliciunguis	Cyprinidae
25. Fridericianella	Ariidae
26. Grubea	Scombridae
27. Gonoplasius	Carangidae
28. Heteromicrocotyle	Carangidae
29. Heteronchocotyle	Carcharhinidae
30. Hemitagia	Serranidae
31. Lethacotyle	Carangidae
32. Linguadactyla	Gadidae
33. Leptobothrium	Scyliorhinidae
34. Leptocotyle	Scyliorhinidae
35. Loimosina	Carcharhinidae
36. Lophocotyle	Nototheniidae
37. Microcotyloides	Lutianidae
38. Macrophyllida	Carcharhinidae
39. Neoaxine	Belonidae
40. Neodiplectanum	Liognathidae
41. Neomazocraes	Clupeidae
42. Octoplectanocotyle	Trichiuridae
43. Ophiocotyle	Clupeidae
44. Paradactylogyrus	Cyprinidae
45. Paradiclybothrium	Acipenseridae
46. Parancyrocephaloides	Dactylopteridae
47. Paragyrodactylus	Cobitidae
48. Pedocotyle	Serranidae
49. Protancyrocephalus	Pleuronectidae
50. Protogyrodactylus	Serranidae
51. Pseudobenedenia	Nototheniidae
52. Pseudohaliotrematoides	Siganidae
53. Pseudolamellodiscus	Sphyraenidae
54. Pseudocotyle	Squalidae
55. Pseudohexabothrium	Rajidae
56. Pseudoanthocotyle	Scombridae
57. Pseudomicrocotyle	Carangidae
58. Pterinotrema	Albulidae
59. Rajonchocotyloides	Rajidae
60. Rhabdosynochus	Centropomidae
61. Spinuris	Rhinobatidae
62. Sprostonia	Squatinidae
63. Rhinobatonchocotyle	Rhinobatidae
64. Trivitellina	Serranidae
65. Vallisiopsis	Carangidae
66. Winkenthugghsia	Gempylidae
67. "Cyclocotyla"	Belonidae

TABLE 9

Genera of Monogenoidea, parasitizing one family of fishes.

Genera	Number of species in genus	Family of fishes-- Hosts	Genera	Number of species in genus	Family of fishes-- Hosts
1. Actinocleidus	23	Centrarchidae	15. Lintaxine	2	Sciaenidae
2. Ancyrocotyle	2	Carangidae	16. Loimos	3	Carcharhinidae
3. Amphibdella	3	Torpedinidae	17. Merizocotyle	3	Rajidae
4. Anchoradiscus	2	Centrarchidae	18. Metamicrocotyle	3	Mugilidae
5. Acanthocotyle	13	Rajidae	19. Mazocraes	5	Clupeidae
6. Calceostoma	3	Sciaenidae	20. Mazocraeoides	3	Clupeidae
7. Capsaloides	4	Histiophoridae	21. Nitzschia	3	Acipenseridae
8. Cemocotyle	2	Carangidae	22. Protomicrocotyle	3	Carangidae
9. Cyclobothrium	3	Labridae	23. Pseudacolpenteron	2	Cyprinidae
10. Dogielius	2	Cyprinidae	24. Pryagraphorus	2	Carangidae
11. Daitreosoma	2	Serranidae	25. Rajonchocotyle	10	Rajidae
12. Heteronchocleidus	3	Cichlidae	26. Rhamnocercus	3	Sciaenidae
13. Hamatopeduncularia	2	Ariidae	27. Tetraonchoides	2	Uranoscopidae
14. Lepidotrema	6	Serranidae	28. Vallisia	2	Carangidae

TABLE 10

Genera Monogenoidea, parasitizing two families of fishes

Genera	Number of species in genus	Family of fishes--Hosts	Number of species of Monogenoidea in a given family
1. Anchylodiscus	3	Plotosidae	2
		Gadopsidae	1
2. Ancylodiscoides	15	Siluridae	11
		Bagridae	5 (4)[1]
3. Axinoides	4	Belonidae	3
		Carangidae	1
4. Diplozoon	5	Cyprinidae	5
		Cobitidae	1 (0)
5. Diclybothrium	2	Acipenseridae	2
		Polyodontidae	1 (0)
6. Diclidophoropsis	3	Macruridae	2
		Sparidae	1
7. Discocotyle	3	Salmonidae	3
		Thymallidae	1 (0)
8. Echinopelma	2	Pomadasyidae	1
		Lutianidae	1
9. Gyrodactyloides	5	Salmonidae	2
		Osmeridae	3
10. Gastrocotyle	3	Carangidae	2
		Scombridae	1
11. Hexabothrium	3	Carcharhinidae	2
		Scyliorhinidae	2 (1)
12. Lithidiocotyle	2	Serranidae	1
		Bramidae	1
13. Murraytrema	2	Sparidae	1
		Catostomidae	1
14. Monocotyle[1]	2	Myliobathidae	1
		Trigonidae	1
15. Microbothrium	3	Squalidae	3
		Carcharhinidae	1 (0)
16. Metahaliotrema	2	Ariidae	1
		Scatophagidae	1
17. Octomacrum	2	Catostomidae	1
		Cyprinidae	1
18. Plectanocotyle	3	Serranidae	1
		Triglidae	2
19. Pseudohaliotrema	3	Sparidae	1
		Siganidae	2

(over)

Table 10 (cont'd)

Genera	Number of species in genus	Family of fishes--Hosts	Number of species of Monogenoidea in a given family.
20. Squamodiscus	2	Serranidae	1
		Sciaenidae	1
21. Tagia	2	Tetrodontidae	1
		Sciaenidae	1
22. Thaumatocotyle	2	Trigonidae	2
		Rajidae	1 (0)
23. Thoracocotyle	3	Cybiidae	2
		Coryphaenidae	1

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[1] The number without brackets in the given table just as in the following tables and in the text indicates the total number of species independently of the fact as to whether or not they are also encountered on other groups--families, orders of hosts; the number in brackets indicates the number of species discovered only in the given group. Thus, from five species of Ancylodiscoides known from Bagridae, four were discovered only in this family and one was also found on Siluridae.

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[1] In the work of Pearse (1949) a new species of Monocotyle, included by us in the total number of Monogenoidea, is described but it is not considered here. The fact is that the description and drawing of this species are such that we are not in a position to determine its generic affinity. If what the author writes about the armature of the attaching disc of the given species in true then it must be something completely new and at any rate not having the slightest relation to the genus Monocotyle.

the present time, that is they are monotypical (Table 8). There is no
doubt that these genera cannot have special significance in the discussion
about the normality (for other possible meanings of this word, see above, nobis) of occurrence
of the Monogenoidea on the families of their hosts because in a number of
cases we deal only with single findings. However, even among this group
there are genera which are often found and which strictly occur only on
fishes of one family, and this, either on one species, as for instance
Linguadactyla, Paradiclybothrium, or even on several--Bychowskyella,
Protancyrocephalus and others. More interesting are the following 28
genera which contain several species and each parasitize one family of
fishes (Table 9) and in such a fashion demonstrate more convincingly that
here occur normal connections between the genus of the parasite and the
family of the host. For 23 genera of monogenetic trematodes it is in-
dicated that they occur on two families of fishes (Table 10). During the
examination of this group of genera we see that part of them parasitize
close, more or less related families of fishes, and part on those which
have absolutely no phylogenetic connection between them whatsoever. One
must note that the related families of fishes on which certain genera of p. 252
Monogenoidea are parasitic are in different degrees of consanguinity with
each other. Thus some, as for instance Siluridae and Bagridae, Cyprinidae
and Cobitidae, Acipenseridae and Polyodontidae, Carcharhinidae and
Syliorhinidae etc. are very close to each other, whereas other families,
even though they are related, are distantly so. For instance Trigonidae
and Myliobatidae or Squalidae and Carcharhinidae and others can be placed
in the latter group. Finally the hosts of Gastrocotyle and Plectanocotyle
are in more distant consanguinous relations. For the hosts of Gastrocotyle,
Carangidae and Scombridae, the consanguinous relations are not even
recognized by everybody; however, as we have already indicated Gregory p. 253
(Gregory, 1951) is undoubtedly right when he unites Carangidae, Scombridae
and certain other families within the group Scombroidei; the data on
parasitism fully agree with his conclusions as will be seen later.

The representatives of distant families of Perciformes are also hosts for Plectanocotyle. One must say that if one species (P. gurnardi Ben. and Hesse) is often encountered on different Trigla then the second (P. elleptica Dies.) was encountered only by Diesing (Diesing, 1850) and actually it should be considered as practically undescribed and possibly not even belonging to the given genus.

Special interest is occasioned by the examination of those genera of Monogenoidea as hosts of which were indicated two families of fishes not connected to each other by consanguinous relations. Let us examine these genera. Anchylodiscus is encountered in Australia and only one species--A. gadopsis Hughes--is indicated for Gadopsis species.[1] We have no basis whatsoever to doubt the determination of the host; however, it is not clear whether A. gadopsis is a representative of the genus

Anchylodiscus because it is described very poorly and requires restudy. Consequently, it is not possible to utilize this case in the question under consideration. Of the four species of *Axinoides*, one--*A. oligoplites* (Meserve) Sproston--is indicated from Carangidae, whereas the rest are encountered on Belonidae. Study of the given species indicates that it is relegated to the genus *Axinoides* erroneously by Sproston and that undoubtedly it should be transferred to the genus *Heteraxine* Yamaguti--*H. oligoplites* (Meserve) Bychowsky *comb. nov.* and, running ahead, we shall indicate that the genus *Heteraxine* basically parasitizes Carangidae. Thus, *Axinoides* actually is related to a group of genera parasitizing only one family of fishes.

The finding of the genus *Diclidophoropsis* on two families of fishes must also be considered untrue. In the examination of the description of *D. taschenbergii* (Parona and Perugia) Sproston, one can ascertain that the attribution of this species to *Diclidophoropsis* is doubtful because the structure of the copulatory organ of the typical shape of *D. tissieri* Gallien sharply differs from the one of *D. taschenbergii*. The indications by the authors of the presence of two vaginal openings among the latter demands verification, because one can suspect from their drawings that they mistook the terminal part of the excretory system for the vaginal orifice (see Parona and Perugia, 1892, page 95, and Table 11, Figure 4). We suppose that the transfer of the species *D. taschenbergii* from the genus *Choricotyle*, which was made by Sproston, (Sproston, 1946) is not supported by the facts and *Diclidophoropsis* must be considered as a genus which occurs only on one family of fishes.

The comparison of the morphology of two species of *Murraytrema* which were discovered on hosts of two different families leads us to the division of this genus into two. Precisely the last circumstance forces us to examine these two species more attentively. The presence of three unarticulated (?) middle plates of the attaching armature of the disc is a characteristic sign of the genus established by Price (Price, 1937b). This sign, however, is insufficiently convincing without special analysis of the correlations of middle plates with the middle hooks. Thus we see that the right and left pairs of the middle hooks of *M. robustum* (Murray) are linked
with the corresponding one of the lateral dorsal connecting plates and the p. 254
middle (ventral) is linked with the latter just as takes place among all Diplectanidae. For the second species--*M. copulatum* Mueller--it is characteristic that the three connecting plates are located and articulate

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[1] The indication of Sproston (Sproston 1946, pages 225 and 524) on the finding of *A. tandani* Johnston and Tiegs on *Gadopsis* species is based on poor acquaintanceship with the work of Hughes (Hughes, 1928) and does not correspond to reality.

with the middle hooks completely differently. Thus the ventral pair of hooks connects with the ventral plate which is homologous to the middle plate of Diplectanidae and *M. robustum*, whereas the dorsal plate, which is divided (in phylogenesis and perhaps in ontogenesis) into two parts, is linked by each separate part with the corresponding dorsal middle hook. Thus, here completely different correlations occur. Without entering into excessive details,[1] we should also indicate in connection with what has been said, that there are all the (necessary, *nobis*) foundations to separate the new genus--*Pseudomurraytrema* Bychowsky *gen. nov.* containing the single species *P. copulatum* (Mueller) Bychowsky *comb. nov.* (from the old genus *Murraytrema*, *nobis*) parasitizing fishes of the family Catostomidae. In connection with this, *Murraytrema* appears to be a monotypical genus encountered only on one family of fishes.

The genus *Tagia* until recently was monotypical, but in 1949 the second species *T. micropogoni* Pearse was described. This was done completely unsatisfactorily and the drawings are such that they force us to doubt the correctness of the attribution of this species to the given genus and that the author had a complete specimen of the worm (Pearse, 1949); therefore, one should consider that *Tagia* must be excluded during further discussion .

Although the genus *Thoracocotyle* is cited as parasitizing two families of fishes it is nevertheless incorrect, just as the indication of its presence on Coryphaenidae is a result of the incorrect attribution to this genus of the type, *T. coryphaenae* Yamaguti, by Yamaguti himself. A special structure of the attaching clamp is characteristic (Meserve, 1938, Table 7, Fig. 43), as well as a different type of armature of the sex system for the present representatives of *Thoracocotyle.* In contrast to them, the form described by Yamaguti has an internal structure typical for *Microcotyle*, and its clamps resemble rather those of *Gastrocotyle*, *Pseudaxine* and others and do not resemble the ones possessed by *Thoracocotyle* at all. In such a fashion *T. coryphaenae* should be transferred into the genus *Microcotyle* (*s. lat.*), whereas the genus *Thoracocotyle* should be transferred into the group encountered only on one family of hosts.

The genus *Metahaliotrema* was encountered by its author on two very distant families (different orders!). Unfortunately we did not have the work of Yamaguti (Yamaguti, 1953) and consequently cannot say anything definite.

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[1] One can suppose that in contrast to *Murraytrema*, *Pseudomurraytrema* has intestinal trunks which merge somewhat away from the posterior end.

The analysis of 23 genera of Monogenoidea reproduced in Table 10 show that 16, i.e., the vast majority are actually encountered on two families of fishes related to each other in varying degrees. Four genera (*Axinoides*, *Diclidophoropsis*, *Murraytrema*, and *Thoracocotyle*) are erroneously indicated for this group and must be ascribed to the genera which are encountered on one family of hosts (here also must be ascribed the new genus *Pseudomurraytrema* separated by us). Of the remaining three genera, the data about the occurrence of two (*Ancylodiscus* and *Tagia*) are not sufficiently authenticated and cannot be utilized and one genus (*Metahaliotrema*) apparently is known with certainty from two unrelated families of fishes.

According to the literary data, thirteen genera of Monogenoidea are encountered each on three families of fishes (Table 11). However, this is not accurate and a detailed study of the material shows that two genera p. 255 must be excluded from this list. Thus, as has already been said, the data on *Diplectanotrema* should not be taken into consideration in the analysis of the normal occurrence, not only because not everything about this genus is clear but also as a result of its discovery on fishes from the New York Aquarium, that is, where natural interrelations could easily be disrupted.

The genus *Diclidophora* is indicated for Clupeidae on the basis of the work of Koratha, (Koratha, 1955b) who described *D. lintoni* from *Brevoortia guntheri* (*B. gunteri*, *nobis*). Koratha found (only, *nobis*) two specimens of this species on one fish. The descriptions of the author arouse significant doubt in the correctness of the attribution of this species p. 256 to the genus *Diclidophora*. Consequently it would be erroneous to take into consideration the indication on Clupeidae and the genus *Diclidophora* should, for the time being, be considered as encountered only on two hosts of two related families.

The remaining eleven genera encountered on three families of fishes are encountered apparently indisputably and eight of them on more or less related ones. Thus, *Cathariotrema* (a single species) is encountered on sharks which are ascribed according to Berg (1940), to the order of Lamniformes; *Heterocotyle*--on the skates of close families; *Hexostoma*, *Gotocotyle*, and *Pricea*--on Scombroidei (according to Gregory), *Lamellodiscus*--on close families of *Percoidae*; *Tetrancistrum* on two families of Percoidei, and Siganidae which even though they are remote from the first, nevertheless they are Perciformes; *Tetraonchus* is encountered on more remote but related groups (Salmonidae plus Thymallidae and Esocidae) which are undoubtedly linked genetically according to Berg (Berg, 1936). Finally, three genera have more complex interrelations with their hosts. The first--*Acolpenteron*--is encountered on two related families (*Catostomidae* and Cobitidae) which are linked with the suborder Cyprinoidei and to that unrelated family of Perciformes--Centrarchidae. The second genus--*Heterobothrium*--consists only of two species of which one is encountered

TABLE 11

Genera of Monogenoidea, parasitizing three families of fishes

Genera	Number of species in genus	Families of fishes--Hosts	Number of species of Monogenoidea in a given family
1. Acolpenteron	5	Catostomidae	1
		Cobitidae	1
		Centrarchidae	1
2. Cathariotrema	1	Lamnidae	1
		Carcharhinidae	1 (0)
		Sphyrnidae	1 (0)
3. Diclidophora	13	Gadidae	11
		Macruridae	1
		Clupeidae	1
4. Dionchus	3	Echeneidae	2
		Carangidae	1 (0)
		Rachycentridae	1
5. Diplectanotrema	1	? Balisidae	1
		? Acanthuridae	1 (0)
		? Pomadasyidae	1 (0)
6. Gotocotyle	4	Carangidae	1
		Bramidae	1
		Cybiidae	2
7. Heterocotyle	5	Trigonidae	3
		Myliobatidae	1
		Rhinobatidae	1
8. Hexostoma	8	Thunnidae	8
		Carangidae	1 (0)
		Scombridae	1 (0)
9. Heterobothrium	2	Tetrodontidae	1
		Bothidae	1
		Pleuronectidae	1 (0)
10. Lamellodiscus	10	Sparidae	6
		Lethrinidae	2
		Nemipteridae	2
11. Pricea	9	Scombridae	1
		Cybiidae	7
		Thunnidae	1
12. Tetraonchus	8	Salmonidae	6
		Thymallidae	2 (1)
		Esocidae	1
13. Tetrancistrum	3	Siganidae	1
		Lutianidae	1
		Ephippidae	1

TABLE 12

Genera of Monogenoidea, parasitizing four-five families of fishes.

Genera	Number of species in genus	Families of fishes--Hosts	Number of species of Monogenoidea in a given family
1. Axine	6	Belinidae	2
		Exocoetidae	3 (2)
		Carangidae	1
		Triglidae	1
2. Cleidodiscus	20	Centrarchidae	15
		Amiuridae	2
		Pimelodidae	2
		Cyprinidae	1
3. Entobdella	7[1]	Trigonidae	2
		Bothidae	2
		Pleuronectidae	1
		Soleidae	2 (1)
4. Diplectanum	12[1]	Serranidae	7
		Sciaenidae	4 (3)
		Sparidae	1 (0)
		Girellidae	1
5. Heteraxine	8	Carangidae	5
		Serranidae	1
		Pomadasyidae	1
		Cybiidae	1
6. Megalocotyle	5	Serranidae	1
		Scorpaenidae	2
		Triglidae	1
		Bothidae	1
7. Octostoma	6	Scombridae	3
		Thunnidae	1
		Bramidae	1
		Sciaenidae	1
8. Trochopus	13[1]	Triglidae	9
		Sparidae	2 (1)
		Haplodactylidae	1
		Scorpaenidae	1
9. Haliotrema	10	Mullidae	6
		Pomadasyidae	1
		Lutianidae	1
		Acanthuridae	1
		Apogonidae	1
10. Pseudaxine	5	Cybiidae	2
		Scombridae	1
		Thunnidae	1
		Carangidae	1
		Sparidae	1 (0)

Footnote to Table 12, Russian page 257

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[1] One species was found on the fish of undetermined order.

on Tetrodontidae and the second on Bothidae and Pleuronectidae (see page 232). It is quite possible that this genus must be divided as Price does (Price, 1943b), and then we will have two monotypical genera parasitizing one or two closely related families of fishes; however, the materials of our co-worker L. F. Nagibina (1953) apparently speak against such a division and consequently *Heterobothrium* is encountered on unrelated families just as *Acolpenteron.*

Most interesting are the data about *Dionchus.* The correlations between the two families of their hosts have already been studied above during the discussion of the hosts of *D. remorae* (MacCallum) (see page 228). However, new data are added to these. Thus, Koratha (Koratha, 1955b) discovered one more species--*D. hopkinsi* Koratha (a synonym of *D. rachycentris* Hargis, 1955, *nobis*)--on the gills of *Rachycentron canadus* L. (Rachycentridae). In his second work the author (1955a) devotes a whole section to the question of the interrelations between *Remora* and *Rachycentron*, basing himself, as he writes, on the hypothesis of Bychowsky concerning the significance of monogenetic trematodes for the study of systematic relations of the fishes. In this section he expressed in detail the views of a number of ichthyologists on the correlations of both genera (more specifically families), and then expressed the data about finding on them representatives of the genus *Dionchus.* The general conclusion of Koratha is the probability of close relations of both genera, although he indicates that the final solution of this question should be left to experimental ichthyology. We suppose that we can even now speak with a sufficient degree of certitude about the indubitable consanguinity of all three (?) families--host representatives of the genus *Dionchus.*

Eight genera of Monogenoidea are indicated as parasitizing four families of fishes (Table 12). There is much that is not clear at the present time in the correlations of species within the limits of these genera, and also with their occurrence on different hosts.

The genus *Axine* contains four species encountered on Beloniformes and one on Carangidae and Triglidae. We did not have the work of Ishii and Sawada (Ishii and Sawada, 1938b) in which the species *A. inada* from Carangidae (*Seriola quinqueradiata* Temm. and Schl.) is described, but according to the data in the work of Sproston (Sproston, 1946) and according to the opinion of Price (Price, 1945) there is no doubt that it is *Axine s. str.* p. 257
The species from Triglidae, (*A. triglae* Beneden and Hesse), was described be Van Beneden and Hesse (Van Beneden and Hesse, 1863) very poorly and even without a drawing. Its true situation is not clear. Thus, it is more probable that *Axine* is encountered on two families of Beloniformes and on p. 258
one of Perciformes, i.e., on two unrelated groups; however, on the first of them in a great number of species and in the second one only singly.

Cleidodiscus is undoubtedly an artificial genus; however, if one takes it in contemporary scope one sees that its basic hosts are Centrarchidae. In addition to that, *Cleidodiscus* is known in a small number of species from Amiuridae and Pimelodidae (Siluridae) close to each other, and also related to the cypriniformid Cyprinidae (but distant from Siluroidae). All the last three families are very distant from the first. Later we shall return to the questions concerning the genus *Cleidodiscus* and its occurrence (see page 476).

Entobdella is encountered on three families of Pleuronectiformes of the suborder Pleuronectoidei and is indicated for Trigonidae. In the literature there is an indication of the finding of *Entobdella* on Scorpaenidae which was not taken into consideration by us in Table 4 or in Table 12 because it is incorrect. The first and only indication concerning this is found in the work of Heath (Heath, 1902) who writes that *E. squamula* is described by him from *Paralichthys californicus* Ayres, and also on *Sebastodes* sp. sp. but considerably more rarely. We are convinced that Heath confused two different species, and the one parasitizing *Sebastodes* sp. sp. apparently belongs to the genus *Benedenia*. Since the finding of two species of *Entobdella* on the skates does not arouse any doubt, [*E. diadema* Monticelli was found by the author of the species on *Trigon violacea* Bonaparte near Italy rarely but in a large number of individuals; *E. bumpsii* Linton was often found on *Pastinachus centrourus* (Mitchill) in Woods Hole near the Island of Labrador--Price (Price, 1939)], one must consider that *Entodbella* parasitizes four families of groups of fishes unrelated and distant from each other (pleuronectiformids and skates).

The authenticity of the finding of representatives of the genus *Diplectanum* on four families of fishes does not arouse any doubt. All these families belong to the suborder Percoidei and have more or less consanguinous links with each other. As basic hosts for the genus, one should consider two families, Serranidae and Sciaenidae, on which 10 of the 12 known species are encountered. In the literature there is another indication which is not included in Table 12 about the finding of *Diplectanum* on Labridae. This indication is erroneous because for Labridae, *Diplectanum pedatum* (Wagener) Diesing is indicated as their parasite . This species which is still practically undescribed (the species should be considered as a *nomen nudum*), was discovered only by Wagener in 1857 and has never been encountered by anyone else. Wagener indicates it as a parasite of *Julis*? (Wagener 1857a, page 99) and all the subsequent authors indicate *Julis* sp. as a host without the question mark. One should suppose that there must be here some sort of error in the determination of the fish; if it were not so, *D. pedatum* would have been found in subsequent research.

The genus *Heteraxine* is encountered on families pertaining to Percoidei, i. e., families which are relatively close to each other.

Even though *Megalocotyle* is indicated for four families of fishes, it is done so apparently erroneously. Thus, *M. rhombi* (Beneden and Hesse) from the gills of *Rhombus maximus* L. should be attributed to the genus *Entobdella* because the basic drawings of Van Beneden and Hesse (Van Beneden and Hesse, 1863), the only ones who had this species in their hands, resemble the representatives of this genus much more than *Megalocotyle*. This is all the more probable since *Entobdella* are characteristic for Pleuronectiformes as we saw before. Thus, for the genus *Megalocotyle* one should consider as hosts the representatives of three families of Perci- p. 259
formes, which are, it is true, sufficiently distant from each other.

The genus *Octostoma* is indicated from Bramidae apparently erroneously because the species described by Parona and Perugia (Parona and Perugia, 1896) under the name of *Octobothrium bramae* has never been since encountered even once though it is attributed by contemporary authors to the genus *Octostoma* (*Kuhnia*), but hardly correctly. The fact is, that if one judges by the generally insufficient description and very schematic drawings of Parona and Perugia, *Octostoma bramae* sharply differs from the rest of the species of the genus by the number of hooks of the male sex armature. As regards the finding of *Octostoma* on Sciaenidae we cannot say anything definite because we did not have the corresponding work of Yamaguti (Yamaguti, 1953). In any case, the genus is characteristic for Scombroidei (according to Gregory), and it should be transferred into the group parasitizing three families.

For *Trochopus*, the finding on Perciformes is characteristic. Basically the species of this genus are encountered on Triglidae and Scorpaenidae, which are close to them, and in addition in more rare cases on two families very distant from each other and from Triglidae.

Two genera are indicated as occurring each on five families of fishes.

Of them, *Pseudaxine* is encountered on four families of the group of Scombroidei, according to Gregory, and in addition to that, one of the species is encountered on Sparidae, also related to Perciformes but somewhat further removed from the first four families.

As regards the genus *Haliotrema*, it is indicated basically on Mullidae and on four more families of Perciformes; but of them, four families are more or less close to each other (they are related to Percoidae) and one (Acanthuridae--*H. xesuri*, Yamaguti) is considerably removed from the first.

As a result of the analysis of 10 genera of Monogenoidea indicated in Table 12 we see the following.

1. Two genera--*Pseudaxine* and *Haliotrema*--are encountered on five families of fishes. Both genera infect representatives of one order and predominantly are encountered in a closely related group of families. At the same time, the basic mass of species of *Haliotrema* is discovered on one family of hosts.

2. Correspondingly, on four families of fishes we encountered four genera--*Diplectanum*, *Heteraxine*, *Trochopus*, and *Entobdella*, The first two genera are found on relatively close families, *Trochopus*--mainly on two closer and more seldom on two more remote families, and finally *Entobdella* on three families related to each other and on one not related with the preceding ones.

3. On three families of fishes are encountered three monogenetic trematodes--*Axine*, *Octostoma* and *Megalocotyle*; in all three cases representatives of the genus are encountered on two consanguinously related families and one family which does not have any close genetic links; the representatives of one of these genera (*Axine*), in the basic mass of species, parasitizes both families of related fishes and only one species is encountered on the third.

4. Finally, the genus *Cleidodiscus* should be considered as artificial; however, it is noted that basically it is encountered on one family of fishes and only in a small number of species on three other families not related to the first.

Three genera--*Calicotyle*, *Squalonchocotyle*, and *Urocleidus* are each indicated on seven families of fishes (Table 13). The first of these genera is undoubtedly located on seven families; namely, on three families of sharks, three--skates and on chimaeras. The data about the finding on Bothidae, of which we spoke earlier, are discarded by us (see page 227). One should indicate that there are no species occurring only on chimaeras; however, there is one species *C. affinis* Scott which is known predominately on them and *Raja fullonica*. The consanguinous relations of the sharks and skates are sufficiently known. As regards their links with Chimaera they are, as is understandable, more distant.

The genus *Squalonchocotyle* is discovered indisputably on six families and basically on five families of sharks related to each other in the wide sense and on one family of skates. The indication of the finding of *Squalonchocotyle* on Serranidae refers to *S. mavori*, described by Linton (Linton, 1940), and actually is based on a misunderstanding as was indicated on page 228 . All in all, one must consider that only six families of Selachii p. 261
are hosts of *Squalonchocotyle*.

TABLE 13

Genera Monogenoidea, parasitizing seven-eight families of fishes.

Genera	Number of species on genus	Families of fishes--Hosts	Number of species of Monogenoidea in a given family
1. Calicotyle	8	Carcharhinidae	1
		Pristiophoridae	1
		Squatinidae	1
		Rhinobatidae	1
		Rajidae	3
		Sphyrnidae	1
		Chimaeridae	1 (0)
2. Squalonchocotyle	27	Carcharhinidae	12
		Squalidae	10 (8)
		Sphyrnidae	6 (5)
		Hexanchidae	1 (0)
		Orectolobidae	1
		Torpedinidae	2 (1)
		Serranidae	1 (0)
3. Urocleidus	39	Centrarchidae	26
		Percidae	3
		Serranidae	4
		Cyprinodontidae	3
		Amiuriidae	1
		Catostomidae	1
		Poecliidae	1
4. Capsala	23	Thunnidae	10
		Histiophoridae	4
		Xiphiidae	1 (0)
		Cybiidae	2
		Coryphaenidae	1 (0)
		Molidae	5
		Diodontidae	1 (0)
		Squalidae	1
5. Tristoma	6	Xiphiidae	3
		Histiophoridae	3 (0)
		Thunnidae	1
		Pleuronectidae	1
		Molidae	3 (0)
		Rajidae	1
		Sphyrnidae	1 (0)
		Carcharhinidae	1 (0)

The genus *Urocleidus*, just as *Cleidodiscus*, should be excluded for the time being from the discussion as being artificial, noting however, that it is basically encountered on perciformids, mainly on Centrarchidae.

Two genera are encountered on eight families of fishes each--these are *Capsala* and *Tristoma* (Table 12). Both genera are too complex to be discussed because of the very intricate synonymies and, in this connection, because of the very contradictory data about their occurrence.

The genus *Capsala* is authentically known from seven families, and data of its finding on Squalidae should be considered erroneous. They are cited in the work of Blanchard (Blanchard, 1847) who found a worm once on *Squalus* sp. in New Zealand which he described under the name of *Tristoma squali*. The attribution of this species to the genus *Capsala* (Price 1938b, 1939 and others) seems to us incorrect. It should rather be considered as a representative of the genus *Tristoma*. As a basis for this serves the drawing from "Le Regne Animal" Cuvier (edition under the editorship of Blanchard and others),where *T. squali* is drawn on Table 36 (Figures 2 and 3, a) with the following text: This is translated by us from the French "This species was taken from the gills of *Squalus* from New Zealand by Mr. Jules Verraux." These drawings show that the species which interests us is equipped with thorns along the edge of the body which are well-developed among representatives of *Tristoma* and *Capsaloides*, but which are absent or weakly developed among *Capsala*. Seven families of the actual hosts of *Capsala* are divided into two groups which have no direct consanguinous links with each other. To the first belong five families (Cybiidae, Histiophoridae, Xiphiidae, Thunnidae, and Coryphaenidae) which, according to Gregory,unite as Scombroidei and to the second--Molidae and Diodontidae; as a matter of fact, in the last family there is no independent species of *Capsala*,and it is possible that this indication is erroneous.

Without any doubt,the genus *Tristoma* is encountered on three families of Scombroidei (according to Gregory), that is on Xiphiidae, Histiophoridae and Thunnidae. One can strongly doubt the correctness of the data about the finding of *Tristoma* on the remaining five families of fishes. Thus, *Tr. uncinatum* Monticelli is indicated for Pleuronectidae. This worm is reported on *Pleuronectes* sp. (?) on the basis of preparations of Leuckart on whose labels there are no data about the location of its finding (Monticelli, 1889). Because this species has not been encountered by anyone else until now,one can suppose that there is here a certain error. The indications of the finding of *Tristoma* on Molidae are obviously erroneous. The finding of *Tr. coccineum* on *Mola mola* according to Price (Price, 1939) is doubtful,and it is possible that the indication to the discovery of *Tr. papillosum* is based on an error of determination (Sproston, 1946). *Tr. fuhrmanni* Guiart is indicated for Rajidae. Actually this species is not described, because Guiart (Guiart, 1938) cites this name but does not give any description; apparently he establishes this species on the basis of the drawing from the textbook of Fuhrmann (Fuhrmann, 1928, Fig. 1) on which there is an indication that this parasite is from *Raja* sp. The data concerning the finding on Sphyrnidae are based on the fact that one sample of the common parasite of *Xiphias gladius*--*Tr. coccineum*--is in the collection of the Washington National Museum from the collection of MacCallum (see Price, 1939) with the indication that it was found on the gills of *Sphyrna zygaena* (L.). Finally, in the index to the literature on Medical and Veterinary Zoology there is an indication of the presence of *Tr. papillosum* on *Carcharias glaucas* (L.), which has never been confirmed by anyone p. 262 (Stiles and Hassall, 1908). Until fresh contemporary data on the finding of representatives of *Tristoma* on families other than Scombroidei are obtained, one must consider that the genus *Tristoma* is characteristic only for the latter.

As regards five genera of Monogenoidea indicated in Table 12, we arrive at the following conclusions.

1. Two genera *Calicotyle* and *Capsala* are encountered on seven families of fishes; the first on Selachii and Holocephali, i.e., on two classes of fishes; and the second on two groups of related families and these groups are not related to each other (Scombroidei + Tetrodontiformes).

2. On six related families of fishes, one genus, *Squalonchocotyle*, is encountered and predominantly on sharks (only one species on skates).

3. One genus of Monogenoidea--*Tristoma*--is encountered on three families of fishes related to each other.

4. The genus *Urocleidus* should be considered basically characteristic for Centrarchidae but should be excluded from further discussion as artificial.

According to the literary data, *Choricotyle* and *Encotyllabe* parasitize nine families of fishes (Table 14). For *Choricotyle* there is another indication on one species--*Ch. pinguis* described by Linton (Linton, 1940) from *Albatrossia pectoralis* (Macruridae) but actually it is a representative of the genus *Diclidophoropsis*, to which this species is attributed by us. The data concerning the occurrence of *Choricotyle* show that this genus was discovered on seven families of the superfamily Percoidae and on 1 other family of Perciformes--Trigilidae, which is rather remote from Percoidae. The information concerning the finding of *Choricotyle* on Clupeiformes are apparently erroneous. These data belong to the often aforementioned Chauhan (Chauhan, 1945) who found two individuals of *Cyclocotyle* (=*Choricotyle*), multaetesticulae Chauhan on the gills of *Pellona* sp. It is possible that there is here an erroneous indication (determination?) of the host.

The genus *Encotyllabe* is known from eight families of Perciformes, among which Sparidae bear the basic part of the species of the genus, and four families do not have species which occur only among them. The indication of the finding of *Encotyllabe* on Salmonidae demands verification, however, it seems to us that it should not be taken into consideration. It is based on the finding of Ishii and Sawada (Ishii and Sawada, 1938a) of a new species of *Encotyllabe* on the gills of *Onchorhynchus masu.* We suppose that Ishii and Sawada were dealing with samples which were consumed with some perciformids--their hosts--and which accidentally were retained in the gill cavity of *Onc. masu* (Brev.)--a typically rapacious fish. This supposition is rendered much more probable by the fact that all Capsalidae, including *Encotyllabe*,are sufficiently mobile (to affect such transfers, *nobis*).

In addition to that, in the list of Japanese Monogenoidea (Yamaguti, 1943) it is indicated that the species of Ishii and Sawada is synonymous with *E. spari* Yamaguti which substantiates our suppositions even more.

The genus *Dactylogyrus* is sufficiently well substantiated from 10 families (Table 14). The obviously faulty data about the presence of the representatives of this genus on *Esocidae* are not included in that table, for it is beyond doubt that these cases are linked with the finding on the pike of the worms from the real host eaten by this fish. As a whole,the following conclusions can be made about *Dactylogyrus*, namely, that this genus is characteristic for Cypriniformes (more exactly for the suborder of Cyprinoidei), on which 212 of the 221 known species are indicated and,as an exception are encountered in other orders, but the latter are not in genetic link with each other nor with the Cypriniformes. p. 263

The genus *Benedenia* is indicated in natural conditions from 15 families (Table 14) and in addition to that it is encountered on 11 families Holocentridae, Malacanthidae, Pomatomidae, Carangidae, Pomadasyidae, Labridae, Acanthuridae, Triglidae, Balistidae, Ostraciidae and Diodontidae in artificial conditions. Of the total number of 26 families, 19 belong to the Perciformes which bear the basic mass of species of *Benedenia.* These undoubtedly are fishes related to a certain degree. Apparently the indi- p. 264
cation of the finding of two species of *Benedenia* on sharks (should be skates, *nobis*) is correct, although it is a distant group of hosts from Perciformes. As regards Holocentridae, Balistidae, Ostraciidae, and Diodontidae,which are indicated as hosts for *Benedenia,* neither carries a single independent species, and at the same time as was indicated above (page 225), they are indisputably related to Perciformes. Finally, the indication of the finding of *Benedenia* on Mugilidae is doubtful. These data are based on the finding of *B. monticelli* only on a sample on the gills of *Mugil auratus* Risso from the Mediterranean Sea and not by the authors themselves (see Parona and Perugia, 1895). There were no additional findings until the present time and one must think that there is an error

TABLE 14

Genera Monogenoidea, parasitizing 9-10 and 15 families of fishes

Genera	Number of species on genus	Families of fishes--Hosts	Number of species of Monogenoidea in a given family
1. Choricotyle	14	Sparidae	5
		Serranidae	1
		Latilidae	1
		Carangidae	1 (0)
		Pomadasyidae	1
		Maenidae	2 (1)
		Triglidae	1
		Sciaenidae	3
		Clupeidae	1
2. Encotyllabe	9	Sparidae	5
		Serranidae	1 (0)
		Latilidae	1 (0)
		Bramidae	1
		Pomacentridae	1 (0)
		Pomadasyidae	1 (0)
		Scorpaenidae	1
		Labridae	1
		Salmonidae	1
3. Dactylogyrus	221	Cyprinidae	208
		Catostomidae	3
		Cobitidae	1
		Anguillidae	2
		Serranidae	1
		Apogonidae	1
		Percidae	2
		Characinidae	1
		Cottocomephoridae	1
		Gasterosteidae	1
4. Benedenia	23	Myliobathidae	2
		Mugilidae	1
		Serranidae	7
		Coryphaenidae	1
		Lutianidae	1 (0)
		Sciaenidae	1
		Carangidae	1
		Sparidae	4
		Ephippidae	1 (0)
		Chaetodontidae	1 (0)
		Scorpaenidae	3
		Tetrodontidae	1
		Girellidae	1
		Hoplegnathidae	1
		Nemipteridae	1

here. Thus, one must recognize that *Benedenia* is characteristic for a wide circle of Perciformes and Tetrodontiformes which are linked with them and is encountered on Myliobatidae which are unrelated to them.

Consequently, of the four genera of monogenetic trematodes represented in Table 14, three--*Choricotyle*, *Encotyllabe*, and *Benedenia*, are characteristic for Perciformes and one--*Dactylogyrus*, for Cypriniformes, although the last two genera are also encountered in single species on families of fishes unrelated to their basic hosts.

The last three genera parasitizing fishes--*Ancyrocephalus*, *Gyrodactylus*, and *Microcotyle*, are characterized by the occurrence on a considerable number of families: in all three cases more than 15.

Thus, the genus *Ancyrocephalus*, which consists at the present time of 36 species is encountered on 23 families of fishes belonging to 7 orders, namely; Scopeliformes--? Scopelidae (1 species of *Ancyrocephalus*); Cypriniformes--Cyprinidae (10 species), Cobitidae (1 species); ? Ariidae (2-1 species); Anguilliformes--? Muraenesocidae (1-0 species); Beloniformes--Belonidae (two species); Mugiliformes--Mugilidae (3-2 species); Atherinidae (1 species); Perciformes--Serranidae (2 species); Priacanthidae (1 species); Percidae (1 species); Lutianidae (1 species); Liognathidae (1 species); Lethrinidae (1 species); Ephippidae (1 species); Drepanidae (2 species); Cichlidae (1 species); Acanthuridae (2-1 species); Gobiidae (1-0 species); Eleotridae (2-1 species); Platycephalidae (4 species); Tetrodontiformes--Balistidae (1 species); Ostracidae (1 species). Just as *Cleidodiscus* and *Urocleidus*, this genus is artificial in its contemporary scope, but just as both above-mentioned ones, it occurs basically on the Perciformes. For the time being it is excluded from the detailed discussion.

In the genus *Gyrodactylus*, from the total volume of the species described about 60 (actually there are many more) are authentically known from 18 families related to 10 orders, namely: Chimaeriformes--Callorhynchidae (1 species of *Gyrodactylus*); Clupeiformes--Salmonidae (2 species); Esocidae (1 species); Cypriniformes--Ameiuridae (1 species); Catostomidae (1 species); Cyprinidae (14-15 species); Cobitidae (15-13 species); Gasterosteiformes--Gasterosteidae (3 species); Gadiformes--Gadidae (8 species and subspecies); Cyprinodontiformes--Cyprinodontidae (2 species); Mugiliformes--Atherinidae (1 species); Ophiocephaliformes--Ophiocephalidae (1 species); Perciformes--Sciaenidae (1 species); Agonidae (1 species); Zoarcidae (1 species); Cottidae (2 species); Blenniidae (1 species); Cyclopteridae (1 species); Comephoridae (1 species); Cottocomephoridae (2 species); Pleuronectiformes--Pleuronectidae (2 species). Thus, one can say about this genus that it is distributed on the most varied families of fishes, some linked consanguinously with each other, and others not at all. One must remember also that undetermined, as far as the species is concerned, representatives of the genera were often encountered on various Amphibia, p. 265
mainly on tadpoles of the genus *Rana* (Sproston, 1946, and others).

Finally, the genus Microcotyle which contains a huge number of species (at the present time 78 species of them have been described) is encountered on 30 families related to three orders: Mugiliformes--Mugilidae (2 species of Microcotyle); Polynemiformes--Polynemidae (1 species); Perciformes--Serranidae (9 species), Priacanthidae (1 species), Apogonidae (1 species), Sillaginidae (2 species), Latilidae (1 species), Pomatomidae (3 species); Carangidae (4 species); Liognathidae (1 species); Pomadasyidae (2-1 species); Sciaenidae (8 species); Lethrinidae (1 species); Sparidae (17-16 species); Maenidae (1 species); Scorpidae (1 species); Chaetodontidae (3-2 species); Cepolidae (1 species); Embiotocidae (2 species); Labridae (4-3 species); Trachinidae (2 species); Pholidae (1 species); Siganidae (3-2 species); Acanthuridae (1 species); Stromateidae (3 species); Gobiidae (1 species); Scorpaenidae (3 species); Hexagrammidae (2 species); Platycephalidae (1 species Cybiidae (1 species). The relations between three orders of the hosts of Microcotyle are undoubtedly consanguinous. Thus, Jordan and Hubbs (Jordan and Hubbs, 1919) consider that Mugiliformes derived from Perciformes particularly from the ancestors of Apogonidae or Amplessidae. Finally, Polynemiformes, as is known, are closely related with Mugiliformes (a number of authors include their only family into one order with Mugilidae, see for instance Gregory 1951). Thus we can consider that Microcotyle is encountered basically on Perciformes and on two orders (families) of fishes related to them.[1]

Before summarizing the totals of our analysis about the occurrence of genera of monogenetic trematodes on the families of fishes, which are their hosts, let us examine one more table (Table 15) analogous to Table 4. During the composition of this table all the corrections made in the preceding text are taken into consideration, and 6 genera are excluded (Anchylodiscus, Ancyrocephalus, Cleidodiscus, Diplectanotrema, Tagia and Urocleidus) for reasons indicated above. On first examination of Table 15 a relatively large number of genera of monogenetic trematodes, occurring in representatives of two and more families of fishes and relating not only to one order--but to two different ones, becomes apparent. An impression is created that the data of the tables speak for relatively insufficiently close interrelationships between the occurrence of genera of Monogenoidea on the families of fishes and the consanguinous relations of the latter. However, this is not so, and in order to be convinced of this we shall

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[1] It is interesting that in a mimeographed (B. B. has roto-worked, nobis) work of one Hawaiian researcher (W. A. Gosline, Unofficial Addendum to the Recent Fish Sections in Berg's Classification of Fishes both Recent and Fossile, 1948) possessed by A. N. Svetovidov Mugiliformes and Polynemiformes in Berg's scope (comprehension, nobis) are included in the order of Perciformes. Apparently this is incorrect, but demonstrates the degree of similarity of all three orders.

TABLE 15

Occurrence of genera of monogenetic trematodes on fishes

Number of Monogenoidea	On 1 genera of fishes	On 2 genera of fishes	On 3 genera of fishes	On more than three genera of fishes	Total genera of Monogenoidea
On genera of 1 family of fishes	81	10	8	1	100
On genera of 2 families of 1 order of fishes		8	2	6	16
On genera of 3 families of 1 order of fishes			3	8	11
On genera of more than 3 families of 1 order of fishes.				8	8
On genera of 2 families of 2 orders of fishes		1	0	1	2
On genera of 3 families of 2 orders of fishes			1	3	4
On genera of more than 3 families of 2 orders of fishes				3	3
On genera of 3 families of 3 orders of fishes			0	0	0
On genera of more than 3 families of 3 orders of fishes.				2	2
On genera of more than 3 families of more than 3 orders of fishes.				2	2
Total	81	19	14	34	148

analyze these data consecutively from the widest occurrence to the narrowest with the reservation that this will force us to make a certain repetition of what has been said before.

The genus *Dactylogyrus* is discovered on four orders of fishes and *Gyrodactylus* on ten. We have already said about the first that it is basically characteristic for the Cypriniformes which is parasitized by 213 species; whereas the remaining 8 known species are encountered on 7 families pertaining to 3 orders. One cannot fail to notice that 208 species are found on one family--Cyprinidae. The second genus is found among 10 orders, which are little or not at all related to each other. The fact that more than one-half of the known species were discovered on Cypriniformes means nothing, because the degree of information about the genus, and particularly of its distribution on marine fishes is completely insufficient p. 266 and its scope beyond doubt is much more significant than what is known to us at the present time.

Two genera, encountered on fishes of three orders--*Microcotyle* and *Benedenia*--basically, as this was shown earlier, are characteristic for Perciformes. Thus, 75 species of *Microcotyle* were found on representatives of this order and only three on the other two. Of the 23 species of *Benedenia*, 20 were discovered on Perciformes, two on Myliobatidae, and one on Mullet and the last is very doubtful. Beryciformes and Tetrodontiformes are also hosts for *Benedenia*, but we do not possess a single independent species of this genus, and both of these orders are closely related to Perciformes.

Capsala, *Calicotyle*, *Entobdella*, are encountered on more than three families of two orders of fishes. The first genus is found mostly on Perciformes--16 species--and also quite normally and in sufficiently great numbers--five species--on Tetrodontiformes which are related to Perciformes. All seven species of *Calicotyle* live on Selachiformes and one in addition to that on Plectognathae (holocephalans, *nobis*), which, nevertheless, among all the fishes are closest to Selachii and are related to one branch of development--Chondrichthyes (Nikolski, 1954). It is interesting that this is the only species of monogenetic trematodes encountered on representatives of different classes (or at any rate subclasses as is supposed by the majority of authors). *Entobdella* lives basically on Mugiliformes (4 species) and more rarely on Selachii (2 species).

Axine, *Acolpenteron*, *Dionchus* and *Heterobothrium* are encountered on three families of two orders of fishes. The first genus parasitizes Beloniformes in a great majority of species (4 species of p. 267 *Axine*) and is known from Perciformes (2 species). The consanguinous relations of these two orders are dubious. *Acolpenteron* is still insufficiently studied but we can consider that it is encountered on clearly unrelated fishes, approximately in the same insignificant number of species

(Cypriniformes--2 species, Perciformes--1 sp.). Enough has been said above about relations of *Dionchus* (see page 256). We see similar relations among *Heterobothrium* (on Tetrodontiformes--1 species, and on Pleuronectiformes--1 species), but it is possible that this genus was created artifically and then the occurrence of the possible two genera really has a "normal" character.

The two genera *Diclidophora* and *Metahaliotrema* were discovered on two families of two orders of fishes. For the first of these genera the occurrence on closely related orders of hosts is characteristic (see page 225), and on one, in the vast majority of the species (Gadiformes--10 species of *Diclidophora*, Macruriformes--1 species). As regards *Metahaliotrema*, this genus is apparently encountered in two completely unrelated families of different orders.

Until now, we were interested in the occurrence of the genera of monogenetic trematodes on different orders of fishes; passing to the analysis of occurrence on one order of fishes we will have to consider again the questions concerning the interrelations of the families.

Choricotyle, *Encotyllabe*, *Squalonchocotyle*, *Pseudaxine*, *Heteraxine*, *Trochopus*, *Diplectanum* and *Haliotrema* were found on four and more families of fishes of one order. The first two genera are characteristic for the suborder Percoidei and in vast majority are encountered on the superfamily Percoidae; in addition to that, one species of the first genus lives on representatives of a distant suborder--Cottoidei. One must note that about one-half of the species of each of the genera are encountered on one family of fishes, Sparidae, which accidentally coincides for both. Further, *Squalonchocotyle* is characteristic for five families of sharks and the majority of species parasitizes Carcharhinidae and Squalidae; sharply differentiated on the basis of occurrence is one species, *S. torpedinis* (Price) which is discovered on skates--Torpedinidae. However, the independence of the last species as established by Price, (Price, 1942) is not altogether clear to us; it is possible that this variation (subspecies?) is *S. abbreviata* (Olsson). *Pseudaxine* parasitizes practically only Scombroidei (all five species, although one of them, in addition to that, is indicated on Sparidae). For the remaining four genera the occurrence on more or less related families also is characteristic, and on one or two of them in a large majority of species. Thus, of the eight species of *Heteraxine*, five are encountered on Carangidae, of 12 species of *Trochopus*--nine on Triglidae (one more on the more closely related family, Scorpaenidae); of 12 species of *Diplectanum*--10 are found on Serranidae and Sciaenidae, of 10 species of *Haliotrema* six occur on Mullidae and three more on relatively close Percoidae.

Eleven genera--*Cathariotrema*, *Pricea*, *Gotocotyle*, *Hexostoma*, *Heterocotyle*, *Lamellodiscus*, *Megalocotyle*, *Octostoma*, *Tetraonchus*, *Tetrancistrum*, and *Tristoma*--are discovered on three families of fishes of one order. Practically all these genera parasitize more or less related families of fishes, for instance, *Tristoma*, *Gotocotyle* and *Pricea* parasitize the Scombroidei (according to Gregory); whereas *Octostoma* basically parasitizes the same hosts (it is also indicated for Sciaenidae). Only three genera--*Cathariotrema*, *Hexostoma*, and *Tetraonchus*--warrant special remarks. The first of them--monotypical--is encountered on three families of sharks which are very close to each other (see page 230). The second is interesting in the fact that one of the eight of its species (*H. grossum*) p. 268 parasitizes representatives of two families of hosts--Carangidae and Thunnidae underlying by this very fact their consanguinous ties and, what is most important for us, substantiating once more the proximity of Carangidae to the rest of the Scombroidei as is accepted by Gregory. Finally, we have already written about the genus *Tetraonchus* (page 256), and its occurrence is an excellent illustration which substantiates the point of view of L. C. Berg concerning the relations of Salmonidae, Thymallidae and Esocidae.

Finally, 16 genera--*Gastrocotyle*, *Echinopelma*, *Hexabothrium*, *Plectanocotyle*, *Diclybothrium*, *Lithidocotyle*, *Monocotyle*, *Gyrodactyloides*, *Squamodiscus*, *Octomacrum*, *Pseudohaliotrema*, *Ancylodiscoides*, *Diplozoon*, *Discocotyle*, *Microbothrium* and *Thaumatocotyle*--are encountered on two families of fishes of one order. The hosts of these genera are generally sufficiently related with the exception of the hosts of *Plectanocotyle*--Serranidae and Triglidae. As a matter of fact, however, this is the only case of the simultaneous occurrence of the representatives of one genus of monogenetic trematodes on these two families of fishes.
Species of the genus *Choricotyle* were also found on them, whereas the representatives of the genus *Trochopus* are also encountered on the families close to Serranidae--Scorpenidae and Triglidae. Apparently there must be closer genetic links between Triglidae than is usually believed. As a matter of fact, the presence of these links is clearly apparent in the phylogenetic scheme of Gregory to which we have often referred.

Summing up the totals of the examination of Table 15 (the occurrence on one family of fishes) does not demand special commentary. We see that a vast majority of genera of monogenetic trematodes is either encountered on one family of fishes (100 genera) or on a group of families related to one or even two and more orders but which are related to each other (40 genera). The degree of consanguinity of the families of hosts is very different, as is understandable, but at any rate it shows the phylogenetic proximity of these families or even the orders in which these families belong. Only eight genera of Monogenoidea are found in unrelated groups of fishes (which is the most interesting for our analysis). The discussion about their occurrence, which was cited above shows that among them one must distinguish three groups with a different nature of relations with their hosts. The first group, to which Axine, Dactylogyrus, and Benedenia belongs, can be characterized as containing genera whose basic mass of species are encountered on related families of fishes, and in addition to that in small numbers on the (hosts, nobis) unrelated to the first ones (and to each other--Dactylogyrus).[1]

The second group of genera (Gyrodactylus, Heterobothrium, Metahaliotrema and Acolpenteron) are characterized by the occurrence of more or less similar small numbers of species (1-2) on different unrelated families of fishes, that is, it does not indicate any normal links between the occurrence of the genera of Monogenoidea and the consanguinous relations of their hosts.

Finally, the third group, to which Entobdella belongs, is distinguished by the fact that here takes place the occurrence of representatives of the genus only on two unrelated (between them) groups of related families and on each one of them in more or less considerable number of species. This group points to a special case of divergence of a species of the genus apparently connected with ecological differentiation. As a matter of fact, p. 269 it is too early to speak about it now because this problem will be evaluated considerably later (see page 301).

Thus, it can be said that it would be more correct to attribute only four genera (second of the examined groups) to the genera of monogenetic trematodes which actually parasitize unrelated families of fishes.

As a result of the examination of the complete material on the occurrence of the genera of monogenetic trematodes on the families and orders of fishes we can consider the following as fully established:

1. The vast majority of genera of monogenetic trematodes is encountered on one genus of fishes or on several related to one family.

2. When representatives of the genera of monogenetic trematodes are found on several families or even orders of fishes it can be shown in a majority of cases that the latter are related to each other.

3. For an insignificant number of genera of monogenetic trematodes which contain predominantly many species, the following characteristics can be observed: a) either the finding of a basic mass of species on related

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[1] As a matter of fact, the genera Ancyrocephalus, Cleidodiscus, and Urocleidus, which were excluded from discussion, can be included in this in this group.

families of fishes and a small number on families not related to the first ones or to each other; b) or the occurrence on two unrelated groups of families and, within the limits of each group, the families which compose it are related to each other.

Only 4 cases form exceptions: the occurrence of the genera Gyrodactylus, Heterobothrium, Metahaliotrema, and Acolpenteron on families of fishes unrelated to each other. However, as was previously indicated, the monolithic nature of Heterobothrium is not clear and the genus Metahaliotrema is poorly known to us and consequently, only 2% of the total number of monogenetic trematodes appear to be authentic exceptions. However, we shall attempt to show that the case of Gyrodactylus is not a simple exception to the general rule.

CHAPTER IV

OCCURRENCE OF FAMILIES OF MONOGENETIC TREMATODES ON THE ORDERS OF THEIR HOSTS--FISHES

p. 27 Before terminating the examination of the materials on the occurrence of monogenetic trematodes of fishes it is necessary to become acquainted with the correlations between the families of worms and the orders of fishes. The data on this subject are reproduced in Table 16. From it, we see that the majority of families of worms is encountered on one to two orders of hosts and, when in large numbers, on one of them in the vast majority of species. These data, however, require clarifications. Thus a number of families is encountered only on one order of their hosts and until the present time have not been discovered on other orders.[1]

Amphibdellatidae, Bothitrematidae, Chimaericolidae, Diclybothriidae, Hexabothriidae, Hexostomatidae, Loimoidae, Microbothriidae, Plectanocotylidae, Protogyrodactylidae, Protomicrocotylidae, Tetraonchidae and Tetraonchoididae, i. e., 13 of the 27 families, pertain here. And one must bear in mind that these families are not equal in volume. Six of them contain only one genus, and with a widely varying number of species (from 1 to 8). So far only one family with the species is known--Bothitrematidae; as should be expected, it is encountered on one family of fishes. One family is known with two species of one genus, Tetraonchoididae--also encountered only on one family of hosts. The family Amphibdellatidae which contains three species of one genus, is also encountered on one family of fishes. Finally, Tetraonchidae and Hexostomatidae, containing eight species each, are encountered each on three families of fishes. Four families of monogenetic trematodes of the group under examination include two genera each, and have similar complexity, with three species each. These are Protogyrodactylidae and Loimoidae, which are encountered on one family of fishes; and Diclybothriidae and Chimaericolidae which were discovered on two families. Protomicrocotylidae and Plectanocotylidae, each containing three genera and five species, are enumerated: the first on two and the second on four families. Finally, Microbothriidae are discovered on four and Hexabothriidae on eight families of hosts.

In order to evaluate the data which have been presented, it is interesting to note not only that the indicated families of Monogenoidea are encountered on fishes of one order, i. e., undoubtedly related to each other in the wide degree, but also, in the case where the monogenetic trematodes are encountered on several families of fishes, in what relations the families p. 271 of hosts are among themselves. Thus, eight of the 13 indicated families of Monogenoidea are subject to discussion from this point of view, namely: Chimaericolidae, Diclybothriidae, Hexabothriidae, Hexostomatidae, Microbothriidae, Protomicrocotylidae, Plectanocotylidae and Tetraonchidae.

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[1] One must take into consideration that the doubtful cases and materials which were discussed in the preceding chapters are excluded from Table 16 *a priori* and consequently will not be discussed here. However, all the known genera are included in it.

Chimaericolidae are discovered on two close families--Chimaeridae and Calliorhynchidae. Acipenseridae and Polyodontidae--hosts of Diclybothriidae, are very close to each other (Berg, 1940.).

Hexabothriidae are encountered on six families of sharks and on three of skates, and on the first there are only representatives of Hexabothriinae and on the second--Rajonchocotylinae, in the scope accepted by Price (Price, 1942). The exception is formed by Squalonchocotyle torpedinis (Price) which are related to the first subfamily but encountered on skates of the family Torpedinidae. Hexabothriidae are widely distributed on sharks; thus, they are discovered on Carcharinidae (15 species of worms), Sphyrnidae (6-5 species), Orectolobidae (1 species), Scyliorhinidae (2-1 species), Squalidae (10-8 species), and Hexanchidae (1-0 species). It is more probable that subsequent research will show that representatives of the family parasitize all sharks without exception. As regards the skates, the Hexabothriidae, if one should set aside S. torpedinis, are discovered mainly on Rajidae (12 species) and are encountered once on Rhinobatidae; further study of this group will show how normal this is. We have already spoken on several occasions about the consanguinous relations between sharks and skates.

Hexostomatidae are indicated from Thunnidae, Cybiidae and Carangidae. Inasmuch as the family contains only one genus, that which has been said about consanguinous relations of the hosts on page 256 can be also applied wholly to the family.

Microbothriidae are encountered on four families of sharks--Squalidae (2 species of one genus of Microbothriidae), Carcharhinidae (1 species common with Squalidae, and in addition 2 species of two genera), Scyliorhinidae (2 species of two genera), and Squatinidae (1 species).

The consanguinous relations of all sharks are well known to everyone; however, the first and the last family are somewhat removed from the two others which are more closely connected to each other (S. Suvorov, 1948). In this connection, the finding of the same species on Squalidae and Carcharhinidae is an important discovery which points to the presence among them of a certain physiological proximity.

Protomicrocotylidae are discovered on Carangidae (4 species and 2 genera of worms) and Sciaenidae (1 species). Generally the relations between these two families of Perciformes are not very close (Gregory, 1951).

Plectanocotylidae are known from Serranidae, Triglidae (2 species), Trichiuridae and Carangidae, i.e., from fishes related to three different suborders of the Perciformes; however, one cannot fail to note that Gregory ascribes Trichiuridae and Carangidae to one branch of development of Perciformes (Gregory, 1951), and Serranidae and Triglidae have certain consanguinous links.

Tetraonchidae are encountered on Salmonidae, Thymallidae and Esocidae. This family, which contains only one genus, has already been indicated (page 256). We shall reiterate that L. C. Berg considered it beyond doubt that the suborder of Salmonoidei, to which the first two families belong, and Esocoidei stand side by side in the system of fishes, and are genetically linked with each other.

Seven families--Anthocotylidae, Calceostomatidae, Dionchidae, Discocotylidae, Gastrocotylidae, Mazocraeidae and Monocotylidae are encountered on two orders of fishes; however, the relations with the hosts in each family are different.

Anthocotylidae are encountered in two families of Perciformes: Carangidae (1 genus, 2 species of worms), and Gemphilidae (1 species); and on one family (Merluciidae) of Gadiformes (1 species). Even though they are far removed from each other, according to the system of L. C. Berg, the first two families can be considered as closely related because Gemphilidae are close to Trichiuridae (they form a single suborder Trichuroidei), whereas the relations of the latter with Carangidae are apparently close (see page 273). Only one widely distributed species, Anthocotyle merluccii Beneden and Hesse--a parasite of Merluccius merluccius (L.)-- is known from the Gadiformes. Gadiformes apparently are in some genetic relation with the Perciformes, as is considered by the majority of contemporary ichthyologists (Svetovidov, 1948).

Calceostomatidae are known from one family of the Perciformes and two families of Cypriniformes. The data about one of the latter demand verification (see page 363). The relations of both orders are not clear, but in any case they are sufficiently distant from each other (Suvorov, 1948; Nikolsky, 1954).

The correlations between the hosts of Dionchidae were examined before because this family contains only one genus (see page 256).

TABLE 16

Occurrence of families of Monogenoidea on orders of their hosts--fishes

Families	Number of genera	Number of species	Order of fishes on which Monogenoidea are found	Number of genera parasitizing them	Number of species parasitizing them
1. Dactylogyridae					
a)Dactylogyrinae	6	228	Cypriniformes	6	228
			Perciformes	2 (0)	7
			Anguilliformes	1 (0)	2
			Gasterosteiformes	1 (0)	1
b)Ancyrocephalinae	26	175	Perciformes	18	113
			Cypriniformes	9 (5)	42
			Tetrodontiformes	3 (1)	4 (3)
			Dactylopteriformes	1	1
			Pleuronectiformes	1	1
			Cyprinodontiformes	1 (0)	4
			Mugiliformes	2 (0)	10 (9)
			Beloniformes	1 (0)	2
			Anguilliformes	1 (0)	1 (0)
			Scopeliformes	1 (0)	1 (0)
c)Linguadactylinae	1	1	Gadiformes	1	1
2. Diplectanidae	8	36	Perciformes	6	33
			Clupeiformes	1	1
			Mugiliformes	1	1
			No data		1
3. Protogyrodactylidae	2	2	Perciformes	2	2
4. Calceostomatidae	4	6	Perciformes	2	2
			Cypriniformes	2	2
5. Monocotylidae	10	25	Selachiiformes	10	25
			Chimaeriformes	1 (0)	1 (0)
6. Loimoidae	2	4	Selachiiformes	2	4
7. Dionchidae	1	3	Perciformes	1	2
			Echeneiformes	1 (0)	2 (1)
8. Capsalidae	13	98	Perciformes	9	71
			Selachiiformes	5 (3)	10 (8)
			Pleuronectiformes	3 (0)	7 (6)
			Tetrodontiformes	2 (0)	8 (5)
			Acipenseriformes	1	3
			Mugiliformes	1 (0)	1
			No data		4
9. Acanthocotylidae	3	15	Selachiiformes	1	13
			Perciformes	?1	?1
			Anguilliformes	1	1

Table 16 (continued)

Families	Number of genera	Number of species	Order of fishes on which Monogenoidea are found	Number of genera parasitizing them	Number of species parasitizing them
10. Microbothriidae	5	7	Selachiiformes	5	9
11. Tetraonchidae	1	8	Clupeiformes	1	8
12. Amphibdellatidae	1	3	Selachiiformes	1	3
13. Tetraonchoididae	1	2	Perciformes	1	2
14. Bothitrematidae	1	1	Pleuronectiformes	1	1
15. Gyrodactylidae	3	59	Cypriniformes	2	29
			Clupeiformes	2 (1)	7
			Chimaeriformes	1 (0)	1
			Gasterosteiformes	1 (0)	3
			Gadiformes	1 (0)	8 (4)
			Cyprinodontiformes	1 (0)	2
			Mugiliformes	1 (0)	1
			Ophiocephaliformes	1 (0)	1
			Perciformes	1 (0)	10
			Pleuronectiformes	1 (0)	2
16. Diclybothriidae	2	3	Acipenseriformes	2	3
17. Hexabothriidae	7	44	Selachiiformes	7	44
18. Chimaericolidae	2	2	Chimaeriformes	2	2
19. Mazocraeidae	6	17	Clupeiformes	3	9
			Perciformes	3	8
20. Hexostomatidae	1	8	Perciformes	1	8
21. Discocotylidae	3	10	Cypriniformes	2	7
			Clupeiformes	1	3
22. Anthocotylidae	3	4	Perciformes	2	3
			Gadiformes	1	1
23. Plectanocotylidae	3	5	Perciformes	3	5
24. Diclidophoridae	7	38	Perciformes	5	20
			Gadiformes	1	11
			Macruriformes	2 (0)	3
			Tetrodontiformes	1	1
			Pleuronectiformes	1 (0)	2 (1)
			Doubtful data		2
25. Microcotylidae	15	115	Perciformes	12	100
			Beloniformes	3 (1)	8
			Mugiliformes	3 (2)	6
			Polynemiformes	1 (0)	1
26. Protomicrocotylidae	3	5	Perciformes	3	5
27. Gastrocotylidae	8	25	Perciformes	7	24
			Mugiliformes	1	1

Footnote to Table 16. page 273

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[1] Here are included Tagia (see page 447); Hemitagia (see page 447), Pterinotrema (see page 439), Allodiscocotyle (see page 447), Cyclocotyla (see page 431), and Ophicotyle (see page 418).

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Discocotylidae are discovered on Clupeiformes and Cypriniformes. Among the Clupeiformes the *Discocotyle* are encountered on Salmonidae and Thymallidae, the close relations of which have already been discussed (page 230). Among Cypriniformes, this family is discovered on Cyprinidae (6 species of two genera), Catostomidae (1 species) and Cobitidae (1-0 species). All three families are closely related (pages 230 - 256). The relations between Clupeiformes and Cypriniformes are not clear, so that it is impossible for the time being to say whether or not they are linked genetically (Suvorov, 1948).

Gastrocotylidae are encountered on eight families of Perciformes. Of these families six (Carangidae, Coryphaenidae, Scombridae, Cybiidae, Bramidae and Thunnidae), on which were discovered 23 species of six genera, belong to the group of Scombroidei according to Gregory. One genus of Gastrocotylidae is encountered on Serranidae and another one on Sparidae.[1] The last two families are somewhat further removed from the first. The only species discovered on the Mugiliformes is *Chauhanea madrasensis* Ramalingam from the gills of Sphyraenidae. The Perciformes and Mugiliformes are in rather close relation (Suvorov, 1948).

Mazocraeidae are encountered almost in the equal numbers of species on Clupeiformes and Perciformes. In origin the Perciformes undoubtedly are linked with the old (phylogenetically older, *nobis*) Clupeiformes (Suvorov, 1948). Among the Clupeiformes the Mazocraeidae are known only on Clupeidae, and on four families: Scombridae (5 species of three genera), Thunnidae (1 species), Bramidae (1 species, see page 259) and Sciaenidae (1 species, see page 259) from the Perciformes. The first three families undoubtedly are closely related and belong to Scombroidei in the understanding of Gregory, as has already been indicated.

Monocotylidae are encountered on skates--Trigonidae (7 species of worms), Rajidae (9-8 species), Myliobatidae (2 species), and Rhinobatidae (3 species); on sharks--Carcharhinidae (2 species), Lamnidae (1-0 species), Sphyrnidae (2-1 species), Pristiophoridae (1 species), and Squatinidae (1 species), and also on Chimaeriformes (Chimaeridae--*Calicotyle affinis* T. Scott, see page 228). As we have already indicated earlier, the interrelations between the sharks and skates are sufficiently close. As for the Chimaeriformes, their relations with Selachiiformes are stated on page 300 . At any rate these two orders are much closer to each other than each of them is to the rest of the contemporary fishes, in spite of the fact that they separated at least in the Devonian. The presence of *C. affinis* on both at the same time corresponds fully with this, and, so to speak, underlies their consanguinous ties.

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[1] The last species in addition to that was also discovered on Scombridae.

Two families of monogenetic trematodes are indicated as occurring on three orders of fishes. The first--Acanthocotylidae--is discovered on Selachiiformes (13 species of one genus of worms on one family of Rajidae), Perciformes (1 species) and Anguilliformes (1 species). The indication of the finding among the Perciformes pertains to *Lophocotyle cyclophora* Braun for which a number of authors indicates *Notothenia* sp. as host (see Johnston and Tiegs, 1922; Sproston 1946, and others). If we turn to the original description of Braun (Braun, 1896) we will see that he writes somewhat differently, thus, in two places in his work he indicates "the collection of Michaelson" (Hamberger Magalhaensische Sammelreise, No. 176, Navarin, Puerto Toro). There are two samples of monogenetic trematodes labelled thus: "probably from the skin of *Notothenia* 20, XII. 92." Thus, we don't have sufficiently serious basis to consider the finding of *L. cyclophora* on the Perciformes and are inclined to think, rather, that it p. 275
is not so. The indication of the Anguilliformes refers to *Enoplocotyle minima* Tagliani, discovered on the skin of *Muraena helena* (L.). We have no basis for doubt in this case, but, nevertheless, this finding remains not quite clear. As a matter of fact, other questions connected with this species will be indicated in detail later (see page 385). Taking into consideration what has been said, we can consider that Acanthocotylidae are apparently encountered not on three orders of fishes, but on two and on one of them as a normal (regular, lawful, *nobis*) exception.

The second family indicated for three orders of hosts is Diplectanidae. It is known from a number of families of perciformids. In addition to that, Yamaguti described two genera from Mugiliformes (*Pseudolamellodiscus*) and from Clupeiformes (*Diplectanocotyle*) (Yamaguti, 1953). As was already indicated, we did not have the given work of Yamaguti and because of that we cannot say anything about both genera. We shall note, however, that we have already spoken about the connection between Mugiliformes and Perciformes, and Clupeiformes are far removed from the latter and from the Mugiliformes. Diplectanidae are discovered on the Perciformes, on Serranidae (14 species of worms), Sciaenidae (8-7 species), Sparidae (7-6 species), Lethrinidae (2 species), Nemipteridae (2 species), Liognathidae (1 species), and Girellidae (1 species). All these families are related to the superfamily Percoidae, and undoubtedly have sufficiently close genetic links.

Microcotylidae parasitizes four orders--Perciformes, Beloniformes, Mugiliformes and Polynemiformes. Microcotylidae are encountered very widely on the Perciformes. Thus, they are discovered on 32 families relating to nine suborders: Percoidei, Blennoidei, Siganoidei. Acanthuroidei, Scombroidei, Stromateoidei, Thunnoidei, Gobioidei, and Cottoidei. So far Microcotylidae are not known from Ophioidei, Ammodytoidei, Trichiuroidei, Tetragonuroidei, Callionymoidei, Anabantoidei, Luciocephaloidei, and Kurtoidei (so far monogenetic trematodes have been studied only on the first three suborders), but there is no doubt that they will be discovered also on these suborders of the Perciformes. The representatives of three closely related genera are found on Beloniformes--*Axine* (4 species), *Neoaxine* (1 species), and *Axinoides* (3 species); the first and last genera live also on the Perciformes (Carangidae and ? Triglidae, see page 257). Two species of *Microcotyle*, one species of the close genus *Diplasiocotyle*, and three species of *Metamicrocotyle* are discovered on Mugiliformes. One species of *Microcotyle* is found on Polynemiformes. The consanguinous relations between the four orders of fishes on which *Microcotyle* are encountered are apparently sufficiently close. Thus, Suvorov (1948) writes that Beloniformes occupy an intermediate position between Cypriniformes and Mugiliformes. At the same time we know that Cypriniformes are closely related to Mugiliformes and Polynemiformes.

Diclidophoridae are known from five orders--Perciformes, Gadiformes, Macruriformes, Pleuronectiformes, and Tetrodontiformes, For the Perciformes, Diclidophoridae are known among eight families relating to Percoidei (all on the superfamily Percoidae with the exception of three species on Labridae, i.e., on the superfamily Labroidae), and on one family of Cottoidei [Triglidae--1 species--*Choricotyle prionoti* (MacCallum) see page 262.] In Gadiformes all species of Diclidophoridae are encountered only on Gadidae, while on Macruriformes--only on the genus *Macrurus.* Thus, on the one hand hosts from the orders Perciformes, Pleuronectiformes, and Tetrodontiformes (see above), which are related to each other; and on the other the closely related Gadiformes and Macruriformes (the last two orders until recently were accepted as one) are characteristic for Diclidophoridae. It is very possible that these two groups are also related although more distantly. Thus, Gregory explains the origin of the Gadidae and Macruridae from Perciformes and A. N. p. 276
Svetovidov, 1948), considers that the latter family is close to Perciformes.

Capsalidae are encountered on 6 orders of fishes--Perciformes, Selachiiformes, Pleuronectiformes, Tetrodontiformes, Acipenseriformes, and Mugiliformes. First of all the finding of representatives of the family on sharks and skates attracts attention and causes perplexity. There is an indication of the finding of three species on sharks: the first of them, *Sprostonia squatinae* (MacCallum) (see page 377), the second--*Microphyllida antarctica* Hughes encountered in Australia on *Mustelus antarcticus.* The author writes that the last form was found on two of one hundred sharks examined (Hughes, 1928). As regards the third species, it is probably an error (see page 261). Thus, although the findings of Capsalidae on sharks are very rare, nevertheless they do not arouse special doubts as to their authenticity. Cases of Capsalidae parasitizing skates are also authentic. They are also very rare. Thus, *Entobdella diademi* Monticelli and *E. bumpsii* Linton were encountered several times (see page 258). *Benedenia pacifica* Guberlet was found once (2 samples) on *Myliobates californicus* (Gill) in Mexico (Guberlet, 1936a, 1936b), and *B. macrocolpae* Lühe twice (5 samples) on *Rhinoptera javanica* Mueller and Henley near Ceylon (Luhe, 1906). Finally *Tristoma fuhrmanni* Guiar (sic), although it was not described in detail, was undoubtedly discovered on *Raja* sp. (see page 261).

Likewise there are no doubts about the finding of Capsalidae on Tetrodontiformes. Thus, five species of *Capsala* are found on Molidae. In addition to that, there is an indication, although a rather dubious one and not taken into consideration in the composition of Table 16, that *Tristoma* was also found on the same family of fishes (see page 261). Likewise the findings of *Benedenia melleni* on the four families of Tetrodontiformes in artificial conditions (see page 224) were not taken into consideration, nor the data about finding *Capsala* on Diodontidae which do not deserve trust (see page 261). At any rate, both the occurrence of a number of species of *Capsala* in nature and the infection in aquaria by *Benedenia* testify to the authenticity of the Capsalidae parasitizing Tetrodontiformes.

Three representatives of the genus *Entobdella* are authentically known on Pleuronectiformes. The existing indications about the finding of Capsalidae of different genera on Pleuronectiformes are apparently erroneous (see pages 258-261). For Acipenseriformes, the indications are known about the presence of three species of *Nitzschia* and two of them apparently are synonyms of the single authentic species--*N. sturionis* (Abildgaard) (Brinkmann, 1952b; Shulman, 1954a ; in addition to that we have material on "*N. superba* MacCallum" from North America, which shows that it is the same *N. sturionis*). The indications of the finding of *Benedenia* on Mugiliformes are doubtful (see page 261).

Thus, Capsalidae are known with certainty from five orders of fishes quite distant from each other. Their basic number is encountered on the most varied families of Perciformes and on orders of fishes which are genetically connected with this order; namely--Tetrodontiformes, and Pleuronectiformes (see also page 316). Along with this, as is apparent from what has been said before, a small number of species of Capsalidae are undoubtedly found on fishes very distant from the Perciformes, that is on sharks, skates, and (Acipenseriformes ?, *nobis*) Acipenseridae.

Gyrodactylidae are authentically encountered on 10 orders of fishes; the majority of their species were in our hands and they were either collected personally by us or by our collaborators. Their classification into orders and families of hosts practically coincides with the ones for the genus *Gyrodactylus* (see page 316) with the addition of five more parasites for Clupeiformes (genus *Gyrodactyloides*) and of one (*Paragyrodactylus*) for Cypriniformes. Just as for the *Gyrodactylus* the parasitizing p. 277 on the most diversified families (orders) of fishes, the ones which are related to each other, just as the unrelated ones--and perhaps there are considerably more of the latter, is characteristic for this family.

Finally, the last family Dactylogyridae is encountered on 12 orders of fishes; however, in order to show more clearly the peculiarities of the distribution of worms pertaining to this family we shall analyze the distribution of the three subfamilies--Dactylogyrinae, Ancyrocephalinae, and Linguadactylinae--separately.

Dactylogyrinae are authentically known from four orders--Cypriniformes (the basic mass of species of all known genera), Perciformes, Anguilliformes, and Gasterosteiformes. Among Cypriniformes these worms are encountered on Cyprinidae (the basic mass of known species), Catostomidae and Cobitidae. These three families are related to the suborder Cyprinoidei and undoubtedly are closely linked genetically (Suvorov, 1948). The representatives of the genus Dactylogyrus are encountered on the remaining orders of fishes (page 262) and one species of Acolpenteron from Centrarchidae (page 256). One must note here only that the two species indicated in the table for Anguillidae--Dactylogyrus bini Kikuchi and D. anguillae Yin and Sproston (discovered on Anguilla japonica), are apparently the same because the differences indicated by the authors are not significant (Yin and Sproston, 1948). In conclusion, one may consider that Dactylogyrinae are characteristic for Cypriniformes and, as exceptions, are encountered on other orders of fishes, but the latter do not have any genetic links with each other or with Cypriniformes.

Ancyrocephalinae (in their contemporary scope, which seems artificial to us, see page 348) are shown as parasitizing 10 orders of fishes (Table 16). Of these orders, the Perciformes bear the majority of species and genera, among which these worms are encountered in the suborders: Percoidei (16 families--101 species of worms), Siganoidei (1 family--4 species), Acanthuroidei (1 family--4-3 species), Gobioidei (2 families--3-1 species), Cottoidei (1 family--4 species). Second in order, judging by the quantity of species of parasites, are Cypriniformes, among them Ancyrocephalinae are encountered on three families of the suborder Cyprinoidei (14 species of worms), and 6 families of Siluroidei (28 species). Ancyrocephalinae are encountered in a small number of species (from 1 to 9) on all the remaining eight orders of fishes. One must note that, among the five (?, nobis) of them there is not a single independent genus of Ancyrocephalinae. Thus, this subfamily of Dactylogyridae is basically distributed among Perciformes and Cypriniformes, not connected with each other by close relations, and in isolated cases are discovered on representatives of other orders whether related or not related with the first two or among themselves.

Linguadactylinae, as is known, are encountered only on Gadiformes (see page 352).

Finally, speaking as a whole about Dactylogyridae we must note that as a rule this family is encountered on two orders--Cypriniformes and

Perciformes, which thus are their basic hosts. In addition to that, separate representatives of this family of monogenetic trematodes, which is the largest in volume, are encountered on nine orders of fishes which have no genetic links with each other or with both of the above-mentioned orders or which have genetic relations with them.

Let us summarize everything that has been said before about the occurrence of families of Monogenoidea on orders of fishes.

1. The occurrence either on one order of fishes or on several p. 278
orders which, however, are genetically linked with each other, is characteristic for 21 families of Monogenoidea (Amphibdellatidae, Anthocotylidae, Bothitrematidae, Chimaericolidae, Diclybothriidae, Diclidophoridae, Diplectanidae,[1] Dionchidae, Gastrocotylidae, Hexabothriidae, Hexostomatidae, Loimoidae, Mazocraeidae, Microbothriidae, Microcotylidae, Monocotylidae, Plectanocotylidae, Protogyrodactylidae, Protomicrocotylidae, Tetraonchidae and Tetraonchoididae).

2. The parasitizing on one order of fishes,or as a single exception on a second order not related to the first,is characteristic for one family (Acanthocotylidae).

3. The finding on a group of related orders in a large majority of genera and species and also a normal parasitizing in a small number of species and genera on two orders not related to each other or to the first group is characteristic for one family (Capsalidae).

4. Parasitizing two orders of fishes which have no genetic links, is characteristic for two families Discocotylidae and Calceostomatidae.

5. The occurrence on many orders of fishes, related as well as unrelated with each other,is characteristic for two families (Dactylogyridae and Gyrodactylidae).

Thus, it becomes clear that of 27 families of Monogenoidea, for 23 generally the presence of normal links between the character of their occurrence and the phylogenetic interrelations of the host is typical, and this was not observed only in four of them. The reasons for the latter lie, as we shall attempt to show later, in that part of these families are artifical on the one hand and on the other that here appear other causal relationships.

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[1] If one does not take into consideration the data about the single finding on Clupeiformes (see page 275).

All in all, one can consider it to be firmly established that for all systematic categories of Monogenoidea, starting with the species and ending with the family, there is a fairly clear correlation between their occurrence on the fishes and the consanguinous relations of the latter.

CHAPTER V

OCCURRENCE OF MONOGENETIC TREMATODES AMONG AMPHIBIA AND REPTILIA

As has already been mentioned, monogenetic trematodes are p. 279 also encountered on amphibians and reptiles. They are representatives of 2 families--Polystomatidae and Sphyranuridae. If we accept the system of the first family proposed by Price (Price, 1939), which basically reflects the natural relations, separating however, *Sphyranura* into a special family (see page 401), then five genera (*Polystoma*, *Parapolystoma*, *Diplorchis*, *Eupolystoma*, and *Sphyranura*) are encountered among Amphibia and three (*Polystomoides*, *Polystomoidella*, and *Neopolystoma*) among reptiles.

Of the five genera under discussion which are encountered among the Amphibia, one (*Sphyranura*) parasitizes caudate amphibians, and the remaining four-- acaudate. The representatives of the genus *Sphyranura* are encountered on Proteidae (in a single species--*Necturus maculosus* Raf.) and Salamandridae (*Eurycea tynerensis* Moore and Hughes), and on the first family (species)--three species, while in the second--one; in each case each species of parasite is encountered only on one species of host. Both families of caudate amphibians are undoubtedly closely related.

As hosts of the genus Polystoma are representatives of the genera *Rana* (with 2 species of *Polystoma*), *Bufo* (2 to 1 species), *Hyla* (4 species), *Rhacophorus* (1 species), and *Xenopus* (1 species). All the described species of *Polystoma* are encountered either on one species of host or on several related to one genus. An exception is *P. integerrimum* Froelich, which was authentically discovered in *Rana temporaria*, *R. arvalis*, *R. agilis*, *R. esculenta*, and *Bufo viridis*.[1] As a whole the genus *Polystoma* is encountered in the representatives of four families related to the suborders of raniformids, bufoniformids, and bombiniformids. If the first two suborders are undoubtedly close, then the bombiniformids and especially Pipidae, to which *Xenopus laevis* Daud. --the host of *P. xenopi* Price is related, are rather sufficiently removed from them (Terentiev, 1950). In becoming familiar with the morphology of *P. xenopi* we see that this species sharply differs from all other species of *Polystoma*. These differences can be summed up as follows. In the first place the intestinal trunks in *P. xenopi* do not form commissures among themselves and do not merge at the posterior end. If the first indication, that is the absence of commissures between the intestinal trunks, is encountered among certain species of

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[1] The indications of the presence of this species on other amphibians is erroneous.

Polystoma and also among other Polystomatidae of acaudate amphibians, the second on the other hand, is characteristic only for this particular species. Thus, if one is to consider the data of Yamaguti (Yamaguti, 1936) as correct, then even among all the Diplorchis the intestinal branches merge p. 280 at the end. In the second place the uterus is absent among P. xenopi and there is only an oötype containing one egg just as among neotenic forms of Polystoma and the representatives of Polystomatidae among reptiles. No (other, nobis) species of this family parasitizing Anura (we are speaking here about "normal" and not neotenic forms) has this feature. Generally, this group expresses the tendency toward elongation of the uterus, which is connected undoubtedly with the peculiarities of the life cycle, particularly with the short period of "expedient" egg-laying (see page 121). Besides these differences there is also one less meaningful: Thus the number of chitinous hooks of the sex armature of P. xenopi is 14 whereas among the remaining species of Polystoma they do not exceed 10; however, this undoubtedly is only a species character. A very important indication would have been the absence of vaginal ducts, which possibly differentiates P. xenopi from other species, but we cannot speak with certainty of this because the species was poorly studied and apparently is known so far only from one specimen (Price, 1943c). We can say with certainty that P. xenopi differs from representatives of the genus Polystoma with various distinguishing features which have a primitive character and, in this connection, it would be quite lawful to separate this species into a special genus Protopolystoma gen. nov., containing, so far one species--P. xenopi (Price, 1943) Bychowsky comb. nov. parasitizing Pipidae.

Representatives of the genus Diplorchis are encountered, one species each in one species of the host--two species in Ranidae (in Rana species), and two in Pelobatidae (in Scaphiopus sp.). Both families are related to different suborders which are not very close to each other.

The genus Eupolystoma is described from Rana species.

Finally the genus Parapolystoma is found only on representatives of the bufoniformid group; one species is known from two species of Hyla (Hylidae) and the other apparently from Bufonidae although this has not been firmly established (the worms were found in the free condition in the pond where the toads of the genus Bufo lived).

Polystomatidae found in reptiles are discovered only on turtles connected with the water medium. The genus Polystomoides, containing nine described species, is indicated from four families--Testudinidae, Cheloniidae, Chelidridae, and Trionychidae, and for the second of them—erroneously, as we shall see later. All the species are indicated as encountered either on one host or on representatives of one genus. Two species, P. ocellatus (Rudolphi) and P. coronatus (Leidy), form an exception. Thus, the first species is known from Emys orbicularis (L.)

(=E. europaea) and is indicated also from Chelonia mydas (L.) and Caretta caretta (L.). The indications to the two last species are clearly erroneous, although they are repeated with persistence in all subsequent references (Sproston, 1946, page 352). Thus, in 1822, under the name of Polystoma mydae some sort of a worm was described (without drawings) from the nasal cavity of Halichelis atra = ? Caretta caretta and (or) ? Chelonia mydas, Kuhl and Hasselt 1822. This species was made synonymous with P. ocellatus by Diesing (Diesing, 1850) without any basis. Apparently P. mydae, which was not described until now in detail and not encountered by anyone later, actually parasitizes Cheloniidae, but in the first place it has no relation to P. ocellatus and in the second place its generic affiliation is still unknown; it is more probable that it is a representative of the genus Polystomoides. Thus, P. ocellatus should be considered as parasitizing only one host. As for P. coronatus, the question about its hosts is more complex. It is undoubtedly widely distributed on representatives of Testudinidae and found on Chelydridae close to them, being related to the same superfamily p. 281
of Cryptodera. In addition to that, this species was indicated for Trionychidae--Amyda ferox (Schm.) and A. spinifera (Le Sueur). The indications pertaining to these hosts seem incorrect to us and they cannot be taken into consideration. The following considerations serve as a basis for this. P. coronatus was described in 1888 from the eastern part of the United States and at first "turtle" was indicated as the host. Later this species was described several times among different species of genera of turtles related to Testudinidae. During the revision of Polystomatidae in 1939, Price made a number of others synonymous with this species, among them P. opacum Stunkard, 1916 from Amyda ferox (Schn.) and Malaclemmys lesueurii (Gray) and P. digitatum MacCallum, 1918, from Aspidonectes (=Amyda) spinifera (Le Sueur). In such a fashion, in addition to Testudinidae two more species of Trionychidae were found to be hosts of P. coronatus. The basis for making the species which were mentioned above synonymous was the personal acquaintanceship of Price with the preparations from the collection of the United States National Museum and Stunkard. P. opacum in these materials was represented by one specimen (cotype) from Malaclemmys lesueurii which turned out to be identical with the customary (typical, nobis) P. coronatus; however, this was not a sufficient reason for making this species synonymous because the basic host of P. opacum is another species--Amyda ferox. Until reexamination of materials from this host it is scarcely in order to make this species synonymous. The affair of P. digitatum is more complex. Price had in his possession 13 specimens of this species of which three were cotypes, all from the basic host, i.e. Amyda ferox. From the work of Price it appears that the number of hooks of the genital armature among these individuals fluctuated greatly. Thus, one specimen of the worm had 17, another--22, the subsequent ones 31, 32, 37, 38 hooks, 3 samples with 24 hooks and 4--with 23. Such huge variability in the number of hooks of the copulatory organ is an impossible thing and we are firmly convinced that here certain errors occur, particularly--the combining of a number of forms of Polystomoides into one species. If one should tabulate all the data reproduced on this

questioned or cited in the works of Price, he will arrive at the following series: 14 hooks in 1 individual, 16 in 3, 17 in 1, 22 in 1, 23 in 4, 24 in 3, 30 in 2, 31 in 1, 32 in 6, 33 in 6, 34 in 4, 37 in 1, 38 in 2, and 40 in 2. This tabulation further strengthens our opinion that Price dealt with more than one species, especially since our data in all monogenetic trematodes show the insignificant numerical variability of the given characteristic. This can be substantiated by the data on *P. coronatus* which is discussed. We had at our disposal our 24 specimens of this species from *Chrysemys* sp. from U.S.A. (Michigan) collected in 1935 by D. Smith. During the verification of the number of hooks of the sex armature we obtained the following figures: with 28 hooks 1 individual, with 29--2, with 30--8, with 31--4, with 32--2, with 33--6, and 35--1, which completely corresponds to the usual degree of variability in the number of chitinous elements of the copulatory organs among monogenetic trematodes. Until the special varification and acquisition of new data, one must consider that *P. coronatus*, just as the genus *Polystomoides* as a whole, are only known from representatives of the superfamily Cryptodira.

The genus *Polystomoidella*, containing only three species, is encountered only on two closely related families--Chelydridae and Kinosternidae. The existing indications of the presence of *P. oblongum* (Wright) in *Chrysemys picta* (Schn.) (Testudinidae) are erroneous as Price correctly pointed out (Price, 1939, page 86).

Finally the genus *Neopolystoma* is indicated from Cryptodira, Pleurodira, and Trionychidea, *i. e.*, it is very widely distributed in all turtles with the exception of Cheloniidae. The remaining species are encountered on one species of host with the exception of *P. orbiculare* p. 282 (Stunkard, 1916) for which is indicated a number of hosts from the family Testudinidae (*Pseudemys* spp., *Chrysemys* spp. and others) and also *Trionyx* (=*Amyda*) *ferox*. The data about the latest hosts are based on finding of *Polystoma aspidonectis* MacCallum in the "nasal cavity," lungs and intestinal tract of *Trionyx ferox* from the New York Aquarium (MacCallum, 1918b). Price made the last species synonymous with *N. orbiculare*. To what extent this is correct we hesitate to say, but the finding of this species on a distant host under artificial conditions forces us to consider these conclusions with reserve. However, as a whole the correctness of the data concerning the finding of *Neopolystoma* on the turtles of the superfamily Trionychoidea does not arouse any doubts, because *N. palpebrae* Strelkov is authentically encountered on a single representative of a superfamily in our fauna--*Amyda sinensis* (Wiegmann). The indication of the finding of *Neopolystoma* on Pleurodira is based on *N. chelodinae* (MacCallum) on *Chelodina longicollis* (Shaw), it is true in aquarium conditions. The entire genus apparently is actually widely distributed among all aquatic turtles.

After becoming briefly acquainted with the nature of occurrence of monogenetic trematodes on amphibians and reptiles we can note that here also are observed the same normalities (regularities, *nobis*) as those which were established by us for the occurrence of Monogenoidea among fishes. This pertains to the occurrence of the species just as the genera of both families. *Oculotrema hippopotami* (Stunkard) about which we have already spoken (see page 219) may be an exception for Polystomatidae.

CHAPTER VI

CERTAIN GENERAL CONSIDERATIONS ABOUT OCCURRENCE AND SPECIFICITY

All that has been said above concerning the occurrence of monogenetic trematodes on their hosts must be subjected to further discussion in order to determine not only the facts of finding certain species and higher taxonomic groupings of parasites on particular systematic groups of the hosts, but also to what degree the normalities (principles or regularities, nobis) thus obtained and their exceptions can be utilized in order to understand the historical correlation between the parasites and their hosts, and for the formulation of the systematics of monogenetic trematodes, i. e., the main problem which stands before the present research. p. 283

However, first we must consider the general questions connected with the so-called problem of specificity for, as every reader understands, everything which has been said before is directly related to this question.

We have already often used the term "specificity" without, however, explaining what is meant by it. Strange as it may seem there is not a single clearly expressed definition of specificity; moreover, the majority of the authors who propose a new definition state, at the same time that other definitions are either inaccurate or even erroneous and methodologically unacceptable. Let us attempt to present briefly the materials on determining the specificity of parasites, with the reservation that primarily we shall utilize Russian works because this question is especially debated in our native literature. The simplest definition of specificity is the definition of V. A. Dogiel, namely that the specificity of the parasites is a "certain conditioning of determined species of parasites to determined species of hosts," with the reservation that specificity can vary a great deal (Dogiel, 1947). However, at the present time this definition is considered insufficient and even erroneous by the majority of parasitologists, and new definitions, much more complicated in comparison with the ones cited above, have been offered (Markov, 1953). Thus, G. C. Markov (1953) writes in his doctoral dissertation: "Specificity is the hereditarily consolitated, relative morphophysiological specialization of the parasite to the host or a determined group of hosts, formed under the influence of the conditions in the existence of the parasite," adding to this that specificity represents a specific characteristic of the species. S. S. Shulman (1954b) defines specificity as "the historically formed, ecologically conditioned, supported by natural selection and hereditarily consolidated adjustment of p. 284 the parasite to its host." Finally A. V. Gussew (1955) gives the following definition of specificity: "Morphophysiologically and ecologically conditioned, historically formed--as a rule under conditions of certain stabilization of the medium, hereditarily consolidated and relatively stable adjustment of determined phases of the life cycle of the parasites to a determined circle of hosts," and in another place of this work--more briefly: "The adaptability of the parasite to life only on a determined circle of hosts is called specificity."

From our point of view, all the "new" definitions (in relation to the definition of V. A. Dogiel) suffer from excessive "erudition" (scholarship) and attempt to include such aspects which could successfully be excluded as self-understood. We believe that whatever be the definition of the meaning of specificity it should be considered as a potential aptitude for determined relations with the host, or, in other words the *ability* (aptitude) to exist on this host. We consciously underline the word "ability," contrasting it with the very fact of existence on or in a determined host. As is well known, the transformation of the aptitude into reality is a complex, contradictory process, taking place only in specific conditions. Consequently one must consider that specificity is a potential possibility toward definite correlations between the parasite and a certain circle of hosts; whereas the realization of this possibility leads to the phenomenon observed in nature or experimentally--occurrence of the parasite on a certain host. In other words, the occurrence of the parasite is the realization of its possibilities of existence on a given host under given concrete historical conditions (which, as is self-evident, are determined by definite ecological conditions).

Let us show by an example the difference between specificity and occurrence. Experiments on *B. melleni* (MacCallum) show that this species is specific for (or, as he means by specificity, is actually limited physiologically to, *nobis*) three orders--Beryciformes, Perciformes, and Tetrodontiformes and in nature they are encountered only on a small number of species of three families of Perciformes (see pages 223-225), that is, the specificity of the given species is far from being fully realized. We can cite a considerable number of examples of similar type but this is hardly necessary as the basis for the difference between the definitions of "specificity" and "occurrence" is quite clear from what has been said above.

When we speak about "the ability of a parasite to exist," under this expression is given a whole number of aspects which are determined by the existence of the animal and determining its existence. Just as any ability toward existence of living organism it is also determined among the parasites by an intricate complex of peculiarities which are historically formed and hereditarially transmitted and arise under the influence of internal and external factors which are in uninterrupted interaction with each other. There isn't the slightest necessity to explain this complex phenomenon in each separate case because it is understood by the very word "existence," and consequently to introduce the different aspects which characterize the existence of the parasites into the definition of specificity is unnecessary. For this reason it seems to us that "new" complex definitions are hardly necessary and do not contribute anything principally new for the understanding of the specificity of parasites for their hosts. One can agree that the definition of V. A. Dogiel is not accurate but there isn't the slightest basis to say that it is erroneous. If one is to examine p. 285 "the new" definitions from the same point of view from which their authors consider them we will be able to detect therein erroneous statements which appear as a result of excessive degrees of caution of the authors attempting to underline their dialectico-materialistic understanding of the phenomena and processes.

Insisting that occurrence is a realization of the potential possibilities of existence on a given host we are not inclined to consider it only as a result of the realization of specificity. In complex interrelations of the biocoenotic pair, parasite-host, numerous interactions often take place, interactions which are conditioned by peculiarities of the host and of the medium which plays a role of no less importance in the realization of the possibility of existence of a determined pair, parasite-host, within given historical conditions. However, drawing the picture of the correlations of specificity and occurrence schematically, we can say with certainty that the latter is delimited more narrowly in connection with the circle of the hosts than the former, in spite of the fact that the manifestation of occurrence is more complex by its nature than specificity.

This thought is not new and was expressed in another form by E. N. Pavlovsky (1946) in the shape of a formula: "the circle of potential hosts of polyphagous parasites is much wider than the specific variety of actual hosts" and J. D. Kirchenblatt (1941) "potential specificity is much wider than the real."

Speaking about specificity one must underline that by it we understand the phenomenon wherein the parasite, finding itself on or in the host, develops normally in it and exists in contrast to those cases when the parasite, even though it survives in a certain host, is not in a condition to continue further normal development, reproduction, etc. therein. Cases like the latter which are rather well-known should be indicated by some other term,(perhaps, nobis) "pseudospecificity" or some other way.

Before speaking about the process of the establishment of specificity of the parasites for their hosts it is also indispensable to note that the scope of specificity is a specific indicator (characteristic, nobis) of a given parasite. In the works of the majority of preceding researchers this is implied but not clearly shown. Thus, even in some of the important works of V. B. Dubinin and S. S. Shulmann about the specificity of separate groups of parasites there is not a single line specifically dedicated to the examination of this question (Dubinin, 1950; Shulmann, 1954b). Moreover, V. B. Dubinin does not examine this question in his works which are especially devoted to the question of determining the species in parasitic animals (Dubinin, 1951, 1954). Exceptions are formed only by J. D. Kirchenblatt and G. S. Markov. The first of them, in the very interesting and little used--although often criticized work about the specificity of parasites for their hosts, indicated that specificity is a characteristic attribute of each species of parasite, that is, it represents a specific character (J. D. Kirchenblatt, 1941). This is more clearly expressed by G. S. Markov in his above-mentioned dissertation. We consider this completely correct and, as we shall attempt to show further, it should be constantly borne in mind by parasitologists during their evaluations in determining to which systematic categories a particular parasite should be ascribed. However, one must warn about excessive positivism (or reliance on, nobis) of this nature which can lead to metaphysical distortions characteristic of the thinking of a number of foreign parasitologists, the most obvious representative of whom is Szidat (Szidat, 1944). A just critique p. 286 of the conceptions of Szidat has already been given by a number of Soviet researchers (Markov, 1948; Dubinin, 1951; Shulmann, 1954b).

The question about the process of the development of specificity of parasites to their hosts is extremely important. In order to understand it, it is first of all indispensable to analyse the historical origin of the biocoenotic pair, parasite-host.

The nature of the origin of the pair, parasite-host, in the given historical period of time is touched upon in a well-known article by E. N. Pavlovsky, "Conditions and factors of the establishment of the parasite in the host organism in the process of evolution" (1946).*

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*Editor's Note

The precise translation of this passage is somewhat different from the interpretation given here and elsewhere, and Bychowsky may have intended a slightly different meaning. Literally, it is translated: "Conditions and factors of the formation of the organism of the parasite by the host in the process of evolution."

Bychowsky may have meant to indicate that the host or rather the milieu offered by the host had something to do with the evolution of the parasitic organism or of the biological entity (organism?) which the host-parasite is: Which, of course, it did. However, in English the phrase, "formation of the organism of the parasite by the host." is awkward and somewhat unclear; therefore, we have translated it as above with the full realization that our translation may not catch an intended nuance of meaning properly. Places where this phrase occurs below are marked with a double asterisk.

From our point of view, the main statement of the author, which deserves very minute attention, is the thesis that the(**) establishment of the parasite in the host organism arises anew each time in the ontogenesis of the corresponding pair, in other words, "the process of effectuation of the organism (adaptation to the host?, *nobis*) by the parasite is synchronous to the present period of evolution of life on earth." It is completely correct that E. N. Pavlovsky underlines that in each case the conditions of the origin of this new pair depend upon "a large number of causes connected with both components of the system, both in their present as *well as in their evolutionary past* (the italics are ours--B. B.). Examining the contemporary processes E. N. Pavlovsky shows that for realization of the process of the formation of the pair, parasite-host, the presence of three groups of factors is necessary: 1) those predisposing the organism to its infection by particular parasites; 2) those determining the possibility (**) of the establishment of a particular parasite in the host individual (actually Bychowsky wrote, "possibility of the formation of the individual by the host of a determined parasite," *nobis*); 3) factors permitting the(**) establishment of the parasite in the host organism (reactions of the exterior medium according to E. N. Pavlovsky).

Thus, according to E. N. Pavlovsky only the combined action "of the triad of factors insures the establishment of the pair, parasite-host." This scheme represents a change of the "triad" proposed earlier by E. N. Pavlovsky and V. G. Gnezdilov (1939) for parasites entering the host organism through the mouth. One cannot fail to note that it represents the reflection of a dialectical conception of the process of transformation of a possibility into actuality and by that very fact produces on the reader a very tempting impression. However, it is indispensable to stop briefly on the questions arising in the examination of each one of the members of the "triad" of Pavlovsky.

Speaking about predisposing factors, as "the first member of the triad," E. N. Pavlovsky refers to such, the peculiarities of the structural, physiological and biochemical nature of the host organism which allow the future parasite to utilize the given organism as a host. In other words, he accentuates the peculiarities of the medium of the first order (in relation to the parasite, see Dogiel, 1947), without explaining especially the peculiarities of the parasite which allow it to utilize a particular medium of the first order. At first glance this is a play on words inasmuch as the statement of the question by Pavlovsky, it would seem, presupposes also the peculiarities of the parasite; however, this is incorrect. To predisposing factors in equal measure must be ascribed also the structural and physiological peculiarities of the future parasite which allow it to utilize a certain organism as a host. Moreover it seems to us that in the first place it is indispensable to consider the peculiarities of the parasite in order to understand the process of establishment of the organism in its host. p. 287 Consequently, it is not accidental that in the general discussions arising about the peculiarities of the host E. N. Pavlovsky has to terminate the section on predetermining factors by passing to the evaluation of the phenomena "from the (standpoint of, nobis) parasite" if one can so express himself (1946, page 296).

The factors determining the possibility of (**) the establishment of the future parasite in the host individual (second member of the triad) were characterized by E. N. Pavlovsky completely insufficiently, and principally inaccurately, if one doesn't speak only about a determined group of internal parasites. According to E. N. Pavlovsky the factors which determine the establishment of the pair, host-parasite, basically are the alimentary (food) correlations between the potential hosts and the natural intermediary hosts of the parasite or other sources of invasion. Actually this is a particular case which is mainly characteristic for endoparasites and even then for far from all of them. The great majority of ectoparasites which have a straight or simple cycle of development reach their future hosts by routes not connected with the feeding of the latter. Similarly a number of endoparasites with a complex cycles of development have an active stage which infects the final host through the skin, that is--also without establishment of alimentary links between the final and the intermediary hosts. Consequently non-alimentary links characterize the factors which determine the possibilities of the establishment of the pair, host-parasite. But as the basic factors in this connection should be considered the ones which lead to the establishment of a contact between the future host and the parasite, or the stages of the life cycle of the first and of the second allowing the possibility of infection. Thus, the second part "of the triad of Pavlovsky" is determined by the internal peculiarities of the host and the parasite just as by the exterior factors of the medium in relation to both of them (medium of the second order according to Dogiel).[1]

Finally, speaking about factors effectuating the (**) establishment of the parasite in the host organism (third part of the "triad of Pavlovsky"), which are determined by E. N. Pavlovsky as a reaction of the exterior medium, one should keep in mind that this is hardly sufficiently accurate because, along with these, the physiological condition of the infective stage of the future parasite, which is conditioned not only and very often not so much by the factors (reactions) of the exterior medium, has great significance. In other words, the third part "of the triad of Pavlovsky" is also subjected to the same normalities (regulations, restrictions, laws, nobis) as the preceding ones.

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[1] In his dissertation, A. V. Gussew writes that the second part "of the triad of Pavlovsky" represents "biocoenotic links" (page 302). This undoubtedly is not accurate or, to say it more correctly, these links represent only a part of the factors which determine the possibility of infection.

Accepting the "triad of Pavlovsky" with the above-mentioned reservations basically as a method of analysis of the process of the formation of the biocoenotic pair "host-parasite" we must also not forget the circumstance that in the process which interests us a huge role is played by factors which predispose a specific organism (parasite, nobis) toward the process of becoming established in the host organism and which are interrelated and in certain measure interconditioned.

Passing to further evaluation of the consideration of E. N. Pavlovsky we must say that his conclusions about the role of chance seems to us based on insufficient analysis of the historical moments[1] of the origin of the biocoenotic pair, host-parasite, and hence incorrect. Actually, p. 288
if one is to evaluate the results of the experiments of E. N. Pavlovsky and E. G. Gnezdilov on infection of the secondary intermediary hosts by broad tapeworm pleurocercoids not peculiar to them E. N. Pavlovsky is fully correct when he speaks about "predisposition of these toward infection by parasites with which they hardly had any encounters in the process of its phylogenesis." We believe, however, that here takes place not chance but a fully natural or normal phenomenon--the manifestation of the peculiarities of the diapason of adaptations of pleurocercoids. Plainly speaking, this is the manifestation of the nature of the "demands" of the parasite toward the conditions of the medium conditioned by their historical transformation (or translating into the language of the preceding considerations--the manifestation of specificity). The chance in a given example is expressed only in the fact of encounter of the new pair, host-parasite, (for instance pleurocercoid--lizard or gecko) and not in the presence of "chance"

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[1] It seems to us that the incorrectly understood correlation of the chance and normality (lawful measure, regulation, principle of B. B., nobis) in the given question led to completely unexpected results. Many practical workers of the Health Department began to accuse E. N. Pavlovsky for his noteworthy generalization about natural transmission of sicknesses in the breeding grounds saying that it disorients them, not allowing them to predetermine (or anticipate, nobis) what measures they should undertake in the exploitation of new regions, for "by chance" unexpected diseases can occur in the latter. But this is completely incorrect! It is precisely the correctly understood teaching of E. N. Pavlovsky which will allow us to regularly foretell the possibility of a specific disease in a specific region after the establishment of common norms of distribution in the natural breeding ground, because as we attempted to show above, the fortuitous in the given case are not "the predisposing" factors but only the "determining."

(fortuitous, nobis) predisposing factors which actually were conditioned historically. In this connection the expression of V. A. Dogiel about the "potential" of parasites (Dogiel, 1947, page 62) is more correct. For pleurocercoids of the broad tapeworm the presence of wide adaptive peculiarities which resulted in (during, nobis) the process of evolution and which allowed them to exploit many of the lowest coldblooded vertebrates as hosts, or in other words that the process of adaptation of the larvae of the broad tapeworm to the hosts was formed historically in such a way that it did not lead to narrow specificity to determined hosts, is beyond any doubt. Consequently, to speak about "fortuitous coincidence of peculiarities" in the present case is completely incorrect. One can speak about chance of the parasitizing of different hosts by pleurocercoids of the broad tapeworm but not in making a medium (permanent?, nobis) of a certain organism as a host,because this process, we repeat, is historically conditioned by the diapason of adaptive peculiarities of the parasite (which do not develop suddenly, but which were formed gradually earlier). The fact that the given process in its present stage does not represent anything new is substantiated by the retention of the morphobiological peculiarities of pleurocercoids without any changes. It is possible that later with the establishment of relatively constant new links between the "old" parasite and the "new" host, new evolutionary potentials will also appear but this is not observed in the present phase of the process. Thus, as "fortuitous" appear not the factors which predispose (**) the parasite toward becoming established in the host organism (here Bychowsky actually says, "by the host," nobis), but the factors which determine this,and among them basically the biocoenotic links between certain animals and conditions of the medium.

Summarizing what has been said before, we think that the research of E. N. Pavlovsky undoubtedly has a progressive significance for the understanding of the process of the establishment (**) of the parasite in the host organism; however, his conclusions demand further reworking and,in certain cases,changes.

p. 289 Analyzing the process of the coming into being (**) of the biocoenotic pair, host-parasite, one must draw attention to those sides of this problem which were not reflected by E. N. Pavlovsky. This,first of all,is a question about ways and means of infection of the future host to which, from our point of view, relatively little attention was allotted, whereas for the analysis of the historical development of the interrelations, parasite-host, this question has paramount significance.

A long time ago K. I Skriabin and R. S. Schultz (1931) proposed to divide the parasitic worms into two groups on the basis of their penetration into the final host. To the first of these groups,which received the name Geohelminths,they ascribed those worms which the host received directly from the surrounding medium and,predominantly,they are parasites which do not have intermediary hosts. To the second group, Biohelminths, are ascribed the species which are transmitted through intermediary hosts through which a specific part of the life cycle of the parasite passes. However, this division, although it has a positive significance from our point of view because it underlies the difference in the methods of infection, is clearly insufficient, without even mentioning the fact that the terms themselves are extremely unsuccessful. V. A. Dogiel proposes to differentiate two means of penetration of parasites into the host organism and, in this connection, to divide the parasites of the two groups--with exogenous or endogeneous methods of penetration. However, it seems to us that it is more important to turn attention to other peculiarities of the means of infecting the host; namely, on the element of activity of a given process. In connection with this, we suppose that the most important biologically is the division of the parasites into two different groups on the basis of their mode of infection of the host, namely: (1) infecting the host by an active larva settling independently on the body of the host or penetrating into it; (2) infecting the host passively by means of the host itself (namely by way of the food through the mouth).

This division bears a different character than the two indicated above but does not represent anything particularly new because it has often been used in parasitological literature (see Pavlovsky, 1946).

To the first group, that is, actively infecting the host, pertains the huge majority of ectoparasites, and particularly the basic mass of monogenetic trematodes. A number of endoparasites are also related here. The second group contains the basic mass of endoparasites and also a small number of ectoparasites (see Dogiel 1947, pages 63-71). In certain cases the infection takes place, so to speak, by a mixed way--in the beginning the parasite actively seeks the host and then the latter swallows it during breathing; undoubtedly this method of infection would be more correctly attributed to the first category. Often, among forms which have alternation of generations, the active method of infection alternates with the passive. Thus, the miracidium of many trematodes penetrates into the first intermediary host actively, whereas the cercaria penetrates into the second passively during the consumption by it of the first; adolescaria penetrate into the final host just as passively. Without entering into the discussion of the details of common normalities of the process of infection, it is indispensable to indicate that in our opinion the two named types of infection have a very important significance for the development of specificity of parasites.

Let us pause briefly on the peculiarities of active infection. The first condition for it is the presence of an actively moving larva possessing adaptations for recognition of the subject which must be "attacked" in order to infect it. The second conditions are the morphobiological p. 290
peculiarities of the given larva which allow it to settle, to attach itself on a

determined host, or to penetrate into its body. Finally, the third is the ability to reach maturity within the given host and to await progeny which can survive or to reach a determined phase of the normal cycle. If the last two conditions refer in equal measure also to forms with passive means of infection, then the first sharply differentiates these two groups. Somewhat exaggerating, it is possible to say that in the first case the parasite "selects the host" and in the second, conversely, the host "picks up" the parasite.

During the active attack of the host, two cases are theoretically possible. Either there is no "selection" and the larva falls on any living being which it encounters and its infection can take place in all cases or partially because of some certain peculiarities of the structure and physiology of the host as well as the parasite itself, or the larva selects a certain object for some characteristics which are not yet known to us (most probably some odors or some other attracting peculiarities of biochemical nature) and infects it mostly in the "obligatory" order so to speak (it is understandable that "errors" are possible and that larvae which attack a particular species of host will not be able to develop further on it because of some combination of their own peculiarities and those of the "unsuccessful host"). If, during the first variation, one can expect the infection of a more or less wide circle of hosts "suitable" to the "demands" of the parasite, then in the second the narrow adaptability to the parasitizing of a limited number of species is much more probable. It is understandable that in all our discussions one must not forget about the role of the external medium (in relation to the larva and the future host) which has a determining significance, for the contact between the larva and the host is possible only under favorable conditions. Both of the "theoretical" cases considered above undoubtedly occur in nature. Thus, we can consider that very many cercariae of digenetic trematodes are quite indifferent to the selection of the second intermediary host where they are transformed into the encysted phase, the adolescaria. There are known cases when the same species of adolescaria is encountered on the most varying invertebrate and vertebrate animals (for instance, of adolescaria of certain Strigeidae and others). However, where the larvae actively penetrate into the final host the second variation, that is, a clearly expressed selective ability apparently takes place as a rule. Consequently, we observe in nature a usually relatively small circle of hosts among species with the active method of infection of the final host. The means of infecting the host apparently reflects different ways of historical formation of the bioceonotic pair, parasite-host, In those cases where parasitism arose from predation, commensalism or space-parasitism, one should consider the active means of infection as primary and where the origin of parasitism was through fortuitous penetration into the digestive system of the host, the passive means is characteristic. Complex cases when the same parasite has different means of infection in different phases of the life cycle are obviously secondary phenomena, as is the phenomenon of alternation of generations (Dogiel, 1947). Although we indicated that a relatively narrow circle of hosts is customary only with active means of infection, historically the process of establishment of specificity in this case took place, as Dogiel correctly considers it, in the course of general parasitology by means of a gradual contraction of the initial wide circle of hosts in connection with the gradual adaptation to a larger or smaller uniformity of food.

We now pass to the questions which were stated earlier about the historical origin of the pair, parasite-host, and about the origin of specificity of the parasites toward their hosts. Answering the first one can say that for the analysis of the historical origin of the pair, parasite-host, it is indispensable to approach the groups which have different ways of infection or in other words, in which the origin of parasitism proceeded differently from different primary peculiarities of their biology. With this, it is indispensable to take into consideration "the triad of Pavlovsky," in relation to the formation of the pair, parasite-host, with those remarks which have been expressed earlier. This triad shows the final results of the history of the origin of the pair, but at the same time reflects not only the contemporary process, but also provides the key to the understanding of the history. Proceeding from what has been said before, further discussion of the question must of necessity be transferred from the realm of generalities to the concrete terrain of the study of the determined group, parasite-host, in our case--to return to monogenetic trematodes and their hosts. The second question that was raised before is closely linked with the first and, if it can be answered immediately in a general form that specificity arises simultaneously with the process of appearance of pair--parasite-host, then the working out of the means of further changes of specificity, as it seems to us, can be also solved only by the analysis of concrete material concerning the specificity group. p. 291

The historical origin of monogenetic trematodes, as will be analyzed further in detail (see page 323), is more probably connected with the period of the separation of fishes as an independent group of classes and consequently the first biocoenotic pairs were, in our case, their ancestors and some sort of ancient fishes, most probably relating to the group Selachii. Without entering at the present time into the question of the origin of monogenetic trematodes, we can consider that ectoparasitism is a primary phenomenon of this group and is characteristic for it from the very beginning of its origin. Thus, the transfer from the free way of life to parasitism characterizes the peculiarities of change of conditions of existence, not of Monogenoidea but of their ancestors. At the same time, undoubtedly they were some sort of dalyellid -like, straight-intestined turbellarian which led a predatory type of life and which changed to the moving habitat on the surface of ancient fishes for feeding on different small invertebrates and perhaps on seaweeds on the latter. Beyond any doubt, this process began often at that time and very wide specificity of these ancestral forms took place. The development of monogenetic trematodes as a group could proceed along the gradual evolution of two peculiarities--feeding at the expense of the host and the appearance of morphological adaptations for attachment to the constantly moving body of the host. It seems to us that these two processes are interrelated and in certain measure interconditioned. The factor which was favorable to the contact between the ancestors of monogenetic trematodes and their hosts was the wide distribution of ancient Selachii in the shallow fresh waters where the ancestors of Dalyellidae mainly lived and where the possibility of mutual occurrence was very great. Theoretically we can represent the progress of changes of the degree of the first wide specificity in the following directions; (1) preservation of wide specificity and (2) gradual development of more and more narrow specificity. It is understandable that with this, complicating factors may also occur, that is, the secondary development of wider specificity and the preservation of a determined degree of specificity for a long time.

Thus, we approach the question about the correlation between p. 292
the phylogeny of the parasites and the phylogeny of their hosts, directly, i.e., (directly?, nobis) to the so-called question about conjugate evolution which is the subject of very lively disputes. By conjugate evolution at the present time is understood a prolonged process of common historical existence of the species of the parasite and host during which changes of the parasite take place simultaneously, or almost simultaneously, with the evolutionary changes of the host on or in which it lives. Hence, it is supposed that consanguinous hosts contain related parasites and the phylogenetic relations of the latter reflect corresponding changes among the former, that is, there is a so-called phylogenetic parallelism between the hosts and their parasites.

Without any doubt the presence of phylogenetic parallelism, in addition to being of considerable interest in itself, would have given into the hands of the researchers a very valuable method of study of various questions connected to the problems of evolution of parasites, their hosts, zoogeography and so forth. However, in order to approach this it is necessary to clarify whether or not actually there is a conjugate evolution of the parasites and their hosts, what is the scope of distribution of this process, whether it is observed, and what are the causes which produce deviations and exceptions from the general rule.

Considerable literature abroad and especially in the Soviet Union is dedicated to the questions of phylogenetic parallelism and the problem of conjugate evolution. We will not dwell especially on it, referring those who are interested to the sources (Ass, 1939; Rubtsov, 1940; Eichler, 1940; Kirschenblat, 1941; Szidat, 1944; Markov, 1948 and 1954 and others), but we must analyze certain questions stated in this literature because they are closely related with the problems interesting us.

G. S. Markov (1948, 1953) gave a very sharp critique of the views of foreign and a number of Soviet authors about conjugate evolution of parasites and their hosts. His considerations are the following:

1) The "theories" of conjugate evolution of foreign authors (Fuhrmann, Eichler, Kellog, Metcalf, Szidat and others) bear a purely autogenetic (self-generating, nobis), obviously idealistic character which detaches phylogenesis from concrete ways of development. It determines these "theories" as "phylogenetic determinism" or as he corrects later "phylogenetic fatalism."

2) The Soviet authors have shown an obvious objectivity because they did not subject the present problem to discussion on a matter of principle (on the basis of some principle?, nobis), but only tried to refine the borders of adaptability of phylogenetic parallelism in the direction of their concretization and narrowing.

3) It is indispensable to replace the metaphysical rule of Fuhrmann which fetishes the role of phylogeny, or the role of ancestry in the evolution, with the seventh rule of ecological parasitology (Dogiel, 1948) which G. S. Markov proposes in the following altered formulation:

a) Under equal (similar, nobis) conditions of existence, ecologically close animals--hosts--possess the greatest similarity of the fauna of their endoparasites independently of phylogenetic parentage. The degree of similarity is determined by the degree of ecological proximity; the phylogenetic consanguinity has a greater significance in the cases when consanguinous animals lead a similar form of life.

b) Formerly ecologically close animals--hosts--which now live in different conditions of existence also possess differences in their endoparasite faunas. p. 293

c) Ecologically distant animals--hosts--having "points of contact" in ecology can, independently of phylogenetic consanguinity, possess certain identical or closely related parasites under similar conditions of existence; the phylogenetic consanguinity strengthens the commonness of the parasite fauna.

d) Ecologically distant animals--hosts-- not having the "points of contact" in ecology possess the least similarity in the endoparasite fauna even in the presence of phylogenetic consanguinity.

One must say that G. C. Markov does not deny the possibility of conjugate evolution of the parasites and their hosts; however, he considers that it is one way, but not the only way, of evolution and that the very phenomenon of parallelism must be examined in a very limited way. He writes: "Its dependence (it means the evolution of the parasites--B. B.) on the evolution of the host is not subjected to doubt, and in a number of cases we actually observe conjugate evolution of the hosts and parasites. However, even in these cases we clearly see that the parasites do not remain unchanged but undergo evolutionary influences because of the medium which is external in relation to the host."

If basically the views of G. C. Markov are to be valued favorably then his separate considerations demand considerable criticism and considerable changes. In addition to that, the "seventh rule of ecological parasitology" and its change by Markov speaks only about endoparasites and does not touch upon ectoparasitic animals to which the monogenetic trematodes, which interest us, are related.

First of all let us dwell on the notorious "rule" or of the "law" of Fuhrmann. In Russian literature it is understood in the formulation of K. I. Scriabin (1923)[1], at the same time this formulation is ascribed in passing to Fuhrmann by N. J. Ass, himself. In N. J. Ass' foreword, which was copied from K. I. Scriabin (page 188), he expressed the views of Fuhrmann and attributed them to the latter having transposed the statement of Scriabin into the text of Fuhrmann (Ass, 1939 page 8). Similarly, G. S. Markov cited in quotation marks "the rule of Fuhrmann" according to the formulation of Scriabin. First of all, it is necessary to examine what Fuhrmann himself said and to compare his formulations with that which appears among Soviet parasitologists under the name of "the rule of Fuhrmann."

After a meticulous analysis of the literature and the mainly factual museum collections of tapeworms of birds, Fuhrmann (Fuhrmann, 1909) came to the following conclusions:

"1. Examining the distribution of numerous species of Taenia in different species of birds we observe a very characteristic phenomenon, that determined species are always encountered only in a determined group of birds and are characteristic for it."

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[1] K. I. Scriabin during the fifth parasitological convention in 1949 said that Fuhrmann expressed to him such a formulation personally. However, there are no publications on this subject and it is hardly permissible to rely on memory, especially since the conversations between K. I. Scriabin and Fuhrmann took place 35 years before the convention.

"2. Various species of bird *Taenia* live always in one of the 26 groups of birds now distinguished by us. During the verification of the correctness of all the data of the authors, it appears that the majority of the species is even more specialized in regard to the place of habitat."

In the work of 1932 on tapeworms of birds Fuhrmann again p. 294 confirms his conclusions, formulating them somewhat differently: "In spite of a more fractional subdivision of all the birds (in comparison with the 26 orders of birds accepted in 1909, 45 are accepted in the work of 1932) (Fuhrmann's generalization of 1909, *nobis*) it remains true that each order of birds possesses its special fauna of cestodes. Among hundreds of *Taenia* of the birds of the entire world which we are determining there has not been a single case contradicting this rule." Just as in the preceding work, Fuhrmann analyzes the literary indications which do not fit this rule and in all cases comes to the conclusion that either there is an error in the determination of the species of the tapeworms or the information of the author does not deserve sufficient trust. Evaluating questions of occurrence of the cestodes of the birds, Fuhrmann further indicates that he does not exclude the possibility of separate cases of finding worms on orders of hosts which are not peculiar to them, but thinks that this can happen very rarely because the identical chemistry of the intestines of the birds can be encountered in different orders very rarely. However, he considers it indispensable to clarify the questions (in these exceptional cases, *nobis*) of whether the parasite is developed normally and whether this is not a case when very close but independent species[1] in these birds are encountered.

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[1] Naturally we do not deny absolutely that a species of *Taenia* of a particular bird order cannot accidentally and as an exception be located in a bird belonging to another order; but if similar cases occur it would be interesting to know whether the parasite in this exceptional habitat shows normal development or not, or whether it is rather a case of a very close species, as happens for instance in *Hymenolepis fraterna* of the rat and *Hymenolepis nana* of man which cannot be distinguished from each other but which nevertheless represent two different species (Fuhrmann, 1932, pages 18-19).

These statements are very interesting because they help us to understand correctly the point of view of Fuhrmann about the normalities (principles, *nobis*) established by him. Not less important are his considerations about the fact that the data on tapeworms do not provide any basis so far, because of their insufficiency, on which to maintain that consanguinous relations of the host play a greater role in the distribution of the parasites than the geographical or ecological factors, although he considers this quite possible. All in all "the rule of Fuhrmann," if one should thus call the cautious conclusions of the author, can be formulated approximately as follows: Each order of birds is characterized by its special tapeworm fauna and as a rule the separate species of the latter are encountered only on a determined order of birds or even adapted to their smaller groupings of classification. The formulation of the "rule of Fuhrmann" in the interpretation of K. I. Scriabin, N. J. Ass, and G. S. Markov is as follows: Each order of birds with a few exceptions is characterized by a specific helminthofauna, the representatives of which cannot parasitize the birds of other orders.

By comparing both formulations we see that in the first place Fuhrmann spoke only about the tapeworm fauna and that the helminthofauna in general was later added to his rule. In the second place he writes that as a rule separate species of tapeworms are encountered only in a determined order of birds, whereas in the text of Scriabin-Ass-Markov there is an indication that "the representatives of the helminthofauna *cannot* (the italics are ours--BB) parasitize *etc.*" The categoric attitude of the last expression bears a completely different character than the definitions of the text of Fuhrmann.

Thus, in its initial form "the rule of Fuhrmann" does not correspond to what is passed as his and the author is not responsible in p. 295
any way for what others have represented as his "rule." Let us note also that to Fuhrmann are ascribed completely unexpected things. Thus, in the work of A. G. Knorre (1937) "the rule of Fuhrmann" is expressed thus: "related parasites in related hosts." Meanwhile if one should examine attentively what Fuhrmann wrote, one will see that this is not at all what he said because the statement quoted by us allows us to consider with certainty that he allowed the possibility of the presence, in different orders of birds, of very close and even almost indistinguishable species, i.e., that related parasites can occur or be in unrelated hosts. This is seen in any example of his work. Thus, close species of tapeworm from the genus *Echinocotyle* are encountered in Anseriformes, Charadriiformes and passerines, that is on completely unrelated birds. There is a large number of examples of such nature in the book of Fuhrmann.

One can only regret that erroneous representations about "the rule of Fuhrmann" are scattered in our literature.

Let us now examine more attentively what "the rule of Fuhrmann" represents, how normal (regular, *nobis*) it is, and whether it can be applied to other groups of parasites in addition to tapeworms.

Properly speaking "the rule of Fuhrmann" underscores only the fact that the occurrence of separate species of bird tapeworms is usually limited to a determined, sufficiently wide circle of hosts--an order of the latter. In his resumé of 1932 are cited materials on all the

875 species of tapeworms known up to that time from 850 species of 41 (sic) orders of birds, showing that there is practically no exception to the rule advanced by him. One can hardly disregard this fact especially since subsequent serious research confirms the same normalities (regularities, principles, nobis) concerning tapeworms parasitizing birds. However, numerous facts are known about the finding of single species on several orders, and these cases form the two types--the first in which the species is encountered in representatives of orders related to each other and the second--on birds which have a close biology and composition of food but which pertain to unrelated orders (M. N. Dubinin, 1950, 1951, 1953b). If one can consider the first type as not contradicting "the rule of Fuhrmann" in essence, the second on the other hand appears as a real exception.

However, before considering this as final, one must say that to Fuhrmann is ascribed (the view, nobis), completely unconvincingly from our point of view, that he "considers the distribution of tapeworms in different orders of birds as something pre-established, congealed, in an arrested state of development, something determined" (Markov, 1948). Where does this idea come from? Is it from the fact that to Fuhrmann was ascribed a statement that: "The representatives (of the helminthofauna of determined orders of birds) cannot parasitize the birds of other orders"? But actually Fuhrmann doesn't say anything definite about the reasons which cause a determined distribution of tapeworms among their hosts but only expresses a supposition that it will be possible to show later that consanguinous relations of the hosts (historical factors) play a more important role than the geographical and ecological factors in the nature of the distribution of separate species of tapeworms in the orders of their hosts--birds. This can hardly be understood as justaposition of "mysterious phylogenesis--biological factors" (Markov, 1948). However, we shall return later to the question on "mysterious phylogenesis" (see page 297).

It seems to us completely correct that to evaluate the causality of the "rule of Fuhrmann" by M. N. Dubinin (1953a); "it is completely normal (regular, nobis) that natural taxonomic groupings of animals (order-family-genus), which more often embrace species which are similar in alimentation and form of life, have a more or less similar parasitofauna and contain a large number of common parasites." These considerations are fully acceptable for many groups of endoparasitic animals to which, in this connection but with different limitations, "the rule of Fuhrmann" can be applied. Thus, the rule generally corresponds to the facts and in the present level of knowledge can be accepted, understandably--not as all-embracing, but as one of the rules about occurrence of endoparasitic animals on their hosts. The categoric nature attributed to it is not legitimate and does not speak against Fuhrmann but against his unusually zealous followers and adversaries. Thus, Charles Darwin cannot be blamed if his teaching is perverted by facist-social darwinists and in the p. 296

same way Fuhrmann must not be blamed for the methodologically harmful statements of Eichler, Szidat, and others. "The rule of Fuhrmann" is independent although there are numerous statements to the effect that he never "invented" anything himself, but only repeated the previously stated views of Braun, Leuckart, and Ehring. The first among them spoke generally that the organisms which feed upon other organisms owe their appearance to the organisms which feed them, that is, that the development of the animal world (and also of predaceousness and of parasitism subsequently) could not precede the appearance of free-living organisms feeding at the expense of unorganized media. A different interpretation should be considered as being far-fetched and it is inadmissible to say, as I. A. Rubtsov (1940) did, that: "If under the 'appearance' of organisms one understands their development, then in the words which were cited were expressed the thought about conjugate evolution of the parasite and the host" (?!). The expression of Leuckart about the frequency of occurrence of parasites among different hosts, which in his opinion depends directly on their consanguinity with the basic host, is related on the other hand to the problem of specificity (see page 245). The method of Ehring can be reduced to the comparison of the fauna of different geographical regions and the evaluation of the significance of the study of interrupted ranges of parasites for the determination of the time of the occurrence of this break (in distribution, nobis), that is, it brings in a completely different circle of questions. As a matter of fact, Fuhrmann also examines the problem of the geographical distribution of tapeworms of the birds, referring directly to Ehring and criticizing him rather sharply (Fuhrmann, 1909, pages 21-23).

However, "the rule of Fuhrmann" can be applied not only to endoparasitic worms but, as is obvious from what has been said before, it can be extended to monogenetic trematodes (see pages 300-320) and to a number of other ectoparasite groups as well (Rubtsov, 1940; Blagoveshensky, 1950, 1953; Dubinin 1953, and others).

Thus, to replace "the rule of Fuhrmann" by the "seventh" statement of ecological parasitology (according to V. A. Dogiel) in any of his interpretations is impossible because the latter cannot be applied to a number of larger groups of ectoparasitic animals the infection of which is not affected by the means of alimentation of their hosts. Consequently the opinion of G. S. Markov is not true in essence; V. A. Dogiel (1948) is not completely right either when he speaks about the undermining of the meaning of "the rule of Fuhrmann" by the data of ecological parasitology. However, if in speaking about endoparasites we would be inclined to agree with M. M. Dubinin about the role of the similar form of life and the alimentation of food in the evaluation of causality "of the rule of Fuhrmann," this is far from being so clear for the ectoparasites. Actually we have p. 297 already shown that in a number of cases in the infection by the same species of parasite, the basic role is played by the physiological consanguinity which finds its reflection in the possibility of cross-hybridization of the hosts or in their consanguinous relations. At the same time, ecological factors obviously play a secondary role. Thus, the same species--*Dactylogyrus difformis* Wagener, is encountered mainly among fishes feeding predominantly on vegetational food [*Scardinius erythrophthalmus* (L.)], but simultaneously and among typically benthopelagic fishes feeding mainly on benthos [*Abramis brama* (L.) and others] and maintaining themselves near the surface of the water and feeding on plankton and air insects [*Alburnus alburnus* (L.)]. In *D. similis* Wagener, for instance, we find fishes with different biology [for instance *Abramus brama* (L.) and *Chondrostoma nasus* (L.)] among its hosts. The number of similar cases can be considerably increased if desired. If this is so, and we have no basis to doubt it, then it is most probable that in the foundations of "the rule of Fuhrmann" lie deeper physiological reasons which find their reflection in natural taxonomic classifications of the host. Beyond any doubt ecological factors played and are playing a considerable role in the formation of these physiological properties and peculiarities, but often already in "skimmed" (reduced, *nobis*) form. Hence, it is clear that we think that "the rule of Fuhrmann" reflects those ecologicophysiological peculiarities of the organisms which were formed during a prolonged historical period and which at the same time were expressed also in the natural system of the host (that is in their evolutionary development and on the nature of the infection of the latter by the separate species of the parasites). Thus, it is not "the mysterious phylogenesis" (Markov, 1948) which determined the distribution of separate species of parasites on their hosts, but both phylogenesis and the distribution of parasites reflect complex historically-formed interrelations between the medium and the animals--hosts, and also between the first, the second, and the separate species of the parasite. However, we reiterate that we are only approaching the questions of phylogenesis of the hosts and of their parasites.

As is apparent from the above-mentioned, "the rule of Fuhrmann" is of rather limited character and can serve in a very limited degree for the purposes which interest us, that is, for the formulation of the natural system of the monogenetic trematodes. Basically, it only helps us in the sense that it enables us to pay attention to the case in the event of finding a determined species of the parasite on species of the animals which are distant from the usual hosts and, at best, to show that there is an error in determining (the determination of, *nobis*) the parasite or the host, or that the distant host actually has certain consanguinous relations with the usual hosts. However, properly speaking, that is all that this rule gives us, although in other connections, partly for zoogeographical problems, it is undoubtedly very valuable.

However, besides "theRule of Fuhrmann" there are other principles (normalities, regularities, *nobis*) which have great relation to the question which interests us about the correlations of the phylogenesis of the hosts with those of their parasites. Without entering into details we must note that conjugate evolution, to a certain degree, or to be more precise--duration of the process--always takes place because it is impossible to visualize the historical development of the parasite without the host, independently of how long and in what ecological conditions the pair, parasite-host exists. The question about phylogenetic parallelism is another matter. First of all, in the latter case such a period of time of mutual existence of p. 298 the pair, parasite-host, is presupposed during which parallel changes of both species or the change of one of them (host) with the preservation in him of the connection of the unchanged other (parasite) are possible. Confirmations favoring such relations among different groups of parasites are cited in a number of works; particularly the article of I. A. Rubtsov (1940) contains considerable material. For monogenetic trematodes at the present time the cases with interrupted distribution of species of parasites and hosts cited in our works (Bychowsky, 1948; Bychowsky and Poliansky, 1953) and also with authentic data about the changes of species of the parasite following historical changes of the species of the host in connection with the falling of the last into new ecological conditions (Bychowsky, 1949, 1951) are convincing examples. Theoretically one can represent the following cases of historical interrelations of the species of the parasite and the host:

1) Just as the host itself, the species of parasite living on some hosts does not undergo any revolutionary changes during a specific (or limited, nobis) historical time;

2) The species of parasite changes evolutionarily, changing into another species or species (pl.) on the same unchanging species of the host;

3) The species of the parasite is preserved during the evolutionary change of the species of the host which diverges giving rise to new species; at the same time the ancient species of the parasite can occur on one or several of the species formed;

4) The species of the parasite parallels, more or less, (is synchronous with) the change of the host; at the same time a new or several new species of the parasite occur in different combinations on the newly formed host species: i.e., either on each of the new resulting species of the host there will be a new species of parasite or in part (of the hosts, nobis) there will be the same new species of the parasite and so forth;

5) The species of the parasite becomes extinct during the prolongation of the existence of the host or during its extinction.

6) The species of the parasite transfers to a new host abandoning the ancient one completely because of some changes of ecological nature;

7) The species of parasite transfers to a new host--new hosts, widening its circle of hosts while preserving the old host;

8) The species of parasites transfers to a new host--new hosts, in connection with the extinction of the old host.

It is possible that there can be other more complex cases but basically one can consider that the relations indicated fit into the enumerated 8 variants. At the same time we do not enter into the discussion of the causes which provoke certain evolutionary changes in the hosts as well as in the parasites because the discussion of the general questions of the formation of species would have sidetracked us too far from the main theme of research.

Strictly speaking, we observe phylogenetic parallelism only in the cases anticipated in points 1 and 4; whereas, all the rest give a different nature of interrelations between the history of the species of the parasite and the host. From this alone it is apparent that the phylogenetic parallelism is a particularity of evolutionary changes of the historical pair, parasite-host. However, this perhaps is true only in theoretical conditions, whereas practically, the case of phylogenetic parallelism is most often encountered and by this very fact represents the basic way of evolutionary changes of parasitic animals? A detailed analysis shows that this is not so and that we can with certainty note in nature the presence of evolutionary changes which fit into the theoretical cases p. 299 indicated in points 1, 2, 3, 4, 6, and 7 and only a few, 5, and 8 cannot be shown in contemporary material. The latter will give us sufficient proofs of more or less particular change along all the possible ways and not only by way of phylogenetic parallelism of the species. In spite of the fact that the absence of parallelism in the evolutionary development between the species of the parasite and the host is encountered more often than its presence, nevertheless basically the occurrence of parasites on their hosts reflects consanguinous relations of the first and of the second and in a vast majority of the cases among the parasites which actively infect their hosts (see page 289), particularly among monogenetic trematodes. Thus, related parasites with the correlations of the 1st, 2nd, 3rd, and 4th types will, as a rule, be encountered on related hosts; in the 5th type the parasite disappears altogether and during the 6th, 7th, and 8th the transfers of the parasite both to related, just as to unrelated, hosts are possible. As the analysis shows in these cases, with the active type of infection we shall have mainly the narrow specificity and the infection of hosts related to the former, and during the passive--a wider specificity and the infection of both the related and just as unrelated hosts, i.e., the degree of consanguinity of the hosts will play a lesser role than the similarity of food and conditions of existence. At the same time, however, one must not forget, as has already been indicated, that the consanguinous relations of hosts find reflection both in a similar form of life and in alimentation whichfacilitates a more rapid transfer of parasites on related hosts.

Summing up, one can consider that the peculiarities of monogenetic trematodes noted by us, starting from their species and ending with their families reflect the schemes of historical interrelations about which we spoke earlier. Consequently,it seems to us that we can make a very definite conclusion in that with the establishment of consanguinous relations of the parasites --particularly of monogenetic trematodes, it is fully possible to utilize the analysis of their occurrence on the hosts as a method of phylogenetic research. This conclusion, as we know,is not new, but the discussion which has been carried out, it seems to us, puts it on a more solid base and allows us to evaluate more critically the results which are obtained when we apply the present method.

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CHAPTER VII

FAUNA OF THE MONOGENOIDEA OF SEPARATE GROUPS OF THEIR HOSTS.

For further analysis of links between the hosts and the monogenetic trematodes encountered on them one must examine the occurrence of the latter from a different point of view, namely--to attempt to examine the nature of the fauna of monogenetic trematodes of definite groups of their hosts in order to determine first their monolithic state or conversely their heterogeneity and then to utilize this for the purpose of refining the phylogenesis of Monogenoidea. At the same time one must not forget the opposite--the possibility of utilizing the data on Monogenoidea for the correction of contemporary conceptions about the phylogenesis of their hosts. Both can be considered fully possible inasmuch as we have already shown the indubitable phylogenetic significance of the nature of the occurrence of monogenetic trematodes. p. 300

All three classes of fishes with which we have to deal--Elasmobranchii, Holocephali and Teleostomi are distinctly separated from each other and the first two, as is known, are encountered from the upper Devonian and the third even from the lower Devonian. Without any doubt the first two classes are much closer to each other than either of them is to Teleostomi. If we look at the fauna of Monogenoidea of these three classes, the first thing that becomes apparent is that both subclasses of monogenetic trematodes are encountered on all three classes of fishes; however, their nature of infection is completely different. Thus, Polyonchoinea, Dactylogyridea and Tetraonchidea are known from Elasmobranchii, Holocephali and Teleostomi; whereas, Gyrodactylidae are encountered practically only on the latter. Likewise among Oligonchoinea, Mazocraeidae are encountered only on Teleostomi, Chimaericolidea exclusively on Holocephali--whereas Diclybothriidae are encountered on representatives of all three classes. However, the general data reproduced are very coarse and do not give the correct idea about the nature of the fauna of Monogenoidea on each order.

So far only five species of Monogenoidea are known on Holocephali. Two of them pertain to the order of Chimaericolidea and make up its entire mass. Thus, this order is fully specific for Holocephali and characterizes it. As regards the three other species, one of them, Callicotyle affinis Th. Scott (order Dactylogyridea), is encountered both on Chimaera monstrosa L. and on Raja fullonica L. (see page 228). Beyond any doubt, in spite of the fact that this species is basically encountered on the first host, it is a parasite which chanced upon Holocephali secondarily and which has a relatively short connection with Holocephali as far as time is concerned. The second species--Gyrodactylus moandrica Mendival-Herrera, is undoubtedly secondary, if not a fortuitous parasite of the holocephalan (Mendival-Herrera, 1946). As regards the third species it was found only once and hasn't been described by anyone (since, *nobis*) (see page 410); one can state with certainty that it pertains to the family Hexabothriidae (order Diclybothriidea). Again it is most probable that this is a secondary parasite of Holocephali. In conclusion, one can consider that the fauna of Monogenoidea of the Holocephali is composed of species characteristic only for this class of fishes and for the fishes belonging to Elasmobranchii, but peculiar basically to the latter genus *Calicotyle* is encountered only on Elasmobranchii just as the species of the family of Hexabothriidae are known only from the representatives of this class). Undoubtedly this underscores the phylogenetic links between Holocephali and Elasmobranchii, although as we have already indicated the transfer of two species of worms from the latter onto the former took place considerably later historically than the appearance of Chimaericolidae on Holocephali. As a confirmation of this, in addition to what has been indicated before, is the fact of the absence of any special adaptations toward parasitizing Holocephali among the three "new" species; whereas, in Chimaericolidae all their organization is very specialized. As a contradiction to the phylogenetic significance of the finding of the species indicated can be proposed the consideration about the commonness of the conditions of existence and biology of *Chimaera* and *Callorhynchus* with sharks and skates; however, this is hardly justified because then we could expect the finding of *Calicotyle* and Hexabothriidae on fundic (bottom, *nobis*) bony fishes with equal success which actually is not observed (see however, page 227). p. 301

As has been indicated before, Elasmobranchii have a fauna of monogenetic trematodes composed of representatives of three orders. At the same time, among Polyonchoinea the monogenetic trematodes of the families Amphibdellatidae, Monocotylidae (the exception was indicated above), Microbothriidae, and Loimoidae parasitize Selachii exclusively; whereas Capsalidae and Acanthocotylidae occur on them and on Teleostei. Let us note beforehand that of all Polyonchoinea, only one family from Selachii (Amphibdellatidae) pertains to the order Tetraonchidea, whereas all the rest--to Dactylogyridea--Monopisthocotylinea. Thus, taking into consideration that there are no Dactylogyrinea on Selachii, we can consider that basically representatives of the more highly organized families of the last order are encountered on them. From the point of view of interrelations of the groups of fishes and at the same time of the phylogeny of the parasites, the greatest interest in represented by both families encountered on Elasmobranchii and on Teleostomi. As regards Capsalidae, among them representatives of the genus *Sprostonia*, *Microphyllida*, *Benedenia*, *Entobdella*, and *Tristoma*[1] parasitize the group of hosts which is under consideration. Of these five genera the first two are encountered only on Selachii and the rest, basically not on them but on the Teleostomi. Thus, only two species of *Benedenia* are known from sharks whereas the remaining 21 (the basic mass of species)--from the Perciformes and Tetrodontiformes connected with the latter.[2] Two species of *Entobdella* are encountered fully authentically on sharks and the remaining on Pleuronectiformes. The data concerning the finding of the genus *Tristoma*, typical for Scombroidei, are very doubtful (see page 261); however, the possibility of such findings is not excluded. Thus, one can consider that the representatives of all three genera beyond any doubt either accidentally chance upon the Selachii (which is most probable for *Tristoma*) or are historically linked secondarily with these fishes and transferred on them p. 302 from Perciformes, Tetrodontiformes and Pleuronectiformes. This transfer is undoubtedly linked not with phylogenetic consanguinity, which is absent in the present cases, but with the commonness of the biology and the places of habitat. This is distinctly visible on representatives of the genus *Entobdella*, the hosts of which lead very similar forms of life. With this one must note another important circumstance, namely, that all Capsalidae are freely moving forms which undoubtedly facilitates their existence on hosts quite diversified in structure and surface. This in its turn facilitates the easy transfer of these worms to other hosts including the ones which are very distant from each other phylogenetically. The two genera of Capsalidae encountered only on Selachii are monotypic. They pertain to the same subfamily (Megalocotylinae), basically peculiar to Perciformes. One can also consider that here takes place a secondary adaptation to parasitizing Selachii; however, apparently in the present case the transfer from Perciformes is more ancient for, after the time of transfer the corresponding species, which undoubtedly separated from *Megalocotyle*-like ancestors, produced sufficiently distinct genera on new hosts.

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[1] We do not take the indication of *Capsala* from the shark, *Squalus* sp. into consideration (see page 261).

In contrast to Capsalidae, Acanthocotylidae as a rule parasitize Selachii, specifically skates. The monotypic genera *Lophocotyle* and *Enoplocotyle* form an exception. As regards the first, its occurrence on Perciformes is doubtful (see page 275), it is possible that it is a parasite of the skates. However, the genus *Enoplocotyle*, separated into a special subfamily, undoubtedly parasitizes the Anguilliformes. As can be surmised from what will be said further on (see page 385), it is quite possible that in the present case we deal with the transfer of parasites in a remote historical period from Selachii to Anguilliformes, with subsequent extreme simplification of structure and with considerable separation from the initial *Anthocotyle*-like ancestors.

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[2] Possibly also on Mugiliformes related to Perciformes (see page 264).

In order to finish with the group of families pertaining to Monopisthocotylinea and parasitizing Selachii, let us pause on three more which are encountered only among these fishes. Of these, Monocotylidae is more diversified in morphological characteristics and comprises a greater number of genera and species; at the same time it is very widely distributed both on sharks and on skates. The circumstance that at the present time Monocotylidae is divided into four well-separated subfamilies points to the considerable antiquity of its parasitizing the given group of hosts and correspondingly--a prolonged time of their common evolution.

The rather numerous family of Microbothriidae, concerning the systematic status of which we cannot say anything definite (see page 385), parasitizes exclusively sharks and selachians which are characteristic for this group.

Finally, Loimoidae parasitize only sharks of two families and are apparently their very ancient parasites (see page 370).

Thus, we see that among Monopisthocotylinea which parasitize the Selachii we can easily distinguish two distinct groups. The first of them, phylogenetically primary, i.e., the beginning of its evolution, or more precisely, of the families which enter it, is connected directly with Selachii. Monocotylidae, Microbothriidae, Loimoidae, and Acanthocotylidae enter into the composition of this group. The second group which is phylogenetically secondary for Selachii comprises only the family Capsalidae.

The only family of Tetraonchidea parasitizing skates-- p. 30
Amphibdellatidae--should also be ascribed to the group which is phylogenetically primary because its representatives are encountered only on Torpedinidae and are undoubtedly their very ancient parasites.

The representatives of one order from Oligonchoinea, namely Diclybothriidae, parasitize Selachii and one family, Hexabothriidae, encountered only on sharks and skates, with the single exception indicated above, is characteristic for them. There is no doubt that this family is also phylogenetically primary for Elasmobranchii.

In conclusion, one can say that Elasmobranchii are characterized as a whole by a very specific, phylogenetically primary fauna of monogenetic trematodes which consists almost completely of strongly separated families, the evolution of which has taken place entirely on the given groups of hosts. Only two of these families transfer to other classes of fishes, and in one case this is undoubtedly linked to phylogenetic relations of the hosts (Monocotylidae) and in the other it is independent of them (Acanthocotylidae). In addition to the primary fauna of Monogenoidea which was indicated, a secondary fauna is also encountered on Elasmobranchii which basically transferred recently from Teleostei. Among these phylogenetically

TABLE 17

Fauna Monogenoidea of separate orders of their hosts--fishes

Order of fishes	Families of Monogenoidea occurrence on them	Number of genera of Monogenoidea	Number of species of Monogenoidea
Selachiformes	Amphibdellatidae	1	3
	Monocotylidae	10	25
	Loimoidae	2	4
	Capsalidae	5	10
	Acanthocotylidae	1	13
	Microbothriidae	5	9
	Hexabothriidae	7	44
Chimaeriformes	Chimaericolidae	2	2
	Hexabothriidae	?1	1
	Gyrodactylidae	1	1
	Monocotylidae	1	1
Acipenseriformes	Capsalidae	1	3
	Diclybothriidae	2	3
Clupeiformes	Diplectanidae	1	1
	Tetraonchidae	1	8
	Gyrodactylidae	2	7
	Discocotylidae	1	3
	Mazocraeidae	3	9
Scopeliformes	Dactylogyridae	1	1
Cypriniformes	Dactylogyridae	15	270
	Calceostomatidae	2	2
	Gyrodactylidae	2	29
	Discocotylidae	2	7
Anguilliformes	Dactylogyridae	2	3
	Acanthocotylidae	1	1
Beloniformes	Dactylogyridae	1	2
	Microcotylidae	3	8
Gadiformes	Dactylogyridae	1	1
	Gyrodactylidae	1	8
	Anthocotylidae	1	1
	Diclidophoridae	1	11
Macruriformes	Diclidophoridae	2	3
Gasterosteiformes	Dactylogyridae	1	4
	Gyrodactylidae	1	3
Cyprinodontiformes	Dactylogyridae	1	4
	Gyrodactylidae	1	2

Table 17 continued

Order of fishes	Families of Monogenoidea occurrence on them	Number of genera of Monogenoidea	Number of species of Monogenoidea
Mugiliformes	Dactylogyridae	2	9
	Diplectanidae	1	1
	? ? Capsalidae	? ? 1	1
	Gyrodactylidae	1	1
	Microcotylidae	3	6
	Gastrocotylidae	1	1
Polynemiformes	Gyrodactylidae	1	1
Ophiocephaliformes	Gyrodactylidae	1	1
Perciformes	Dactylogyridae	20	120
	Diplectanidae	6	33
	* Protogyrodactylidae	2	2
	Calceostomatidae	2	4
	Dionchidae	1	2
	Capsalidae	9	71
	Acanthocotylidae	1	1
	* Tetraonchoidae	1	2
	Gyrodactylidae	1	10
	Mazocraeidae	3	8
	* Hexostomatidae	1	8
	Anthocotylidae	2	3
	* Plectanocotylidae	3	5
	Diclidophoridae	5	20
	Microcotylidae	12	100
	* Protomicrocotylidae	3	5
	Gastrocotylidae	7	24
Dactylopteriformes	Dactylogyridae	1	1
Pleuronectiformes	Dactylogyridae	1	1
	Capsalidae	3	7
	Bothitrematidae	1	1
	Gyrodactylidae	1	1
	Diclidophoridae	1	1
Echeneiformes	Dionchidae	1	2
Tetrodontiformes	Dactylogyridae	3	4
	Capsalidae	2	8
	Diclidophoridae	1	1

secondary parasites of Selachii only a few forms separated to the degree of independent genera, but the majority at best reached the degree of well-delineated species. This secondary fauna does not give us basis to speak about phylogenetic links between Elasmobranchii and Teleostei, but the entire fauna of Monogenoidea of Selachii shows that its appearance took

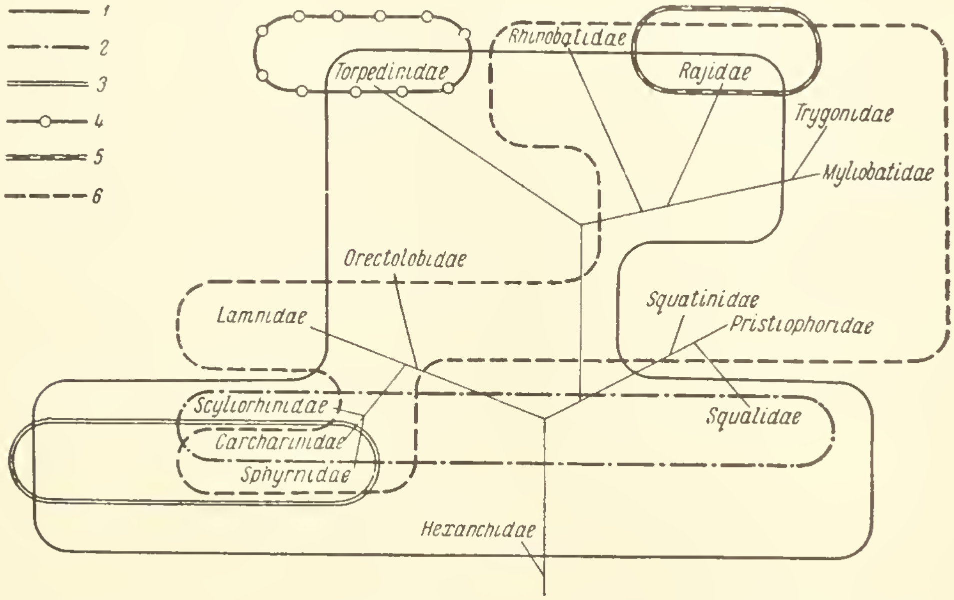

Fig. 262. Diagram of occurrence of monogenetic trematodes on the families of Selachii. The diagram of phylogenetic relations of Selachii is drawn according to Suvarov, 1948. Only the families on which monogenetic trematodes are encountered are retained in it. 1--Hexabothriidae; 2--Microbothriidae; 3--Loimoidae; 4--Amphibdellatidae; 5--Acanthocotylidae; 6--Monocotylidae.

place not before the separation of this class of fishes, but after its formation. However, we shall return to the last question somewhat later (see page p. 305
449). An important circumstance which we can see during the analysis of the fauna of Monogenoidea of Selachii is that it practically consists of a number of families which developed independently and which are not connected with each other by close phylogenetic links and each of which became adapted to parasitizing the present groups of hosts independently from the others. Such beyond any doubt are Amphibdellatidae, Acanthocotylidae, Hexabothriidae, and Microbothriidae. As regards Monocotylidae and Loimoidae, even though one can allow the commonness of origin,there are nevertheless many more bases to think that it is lacking. The phylogenetic origin of their fauna on Selachii undoubtedly is of great significance to the analysis of the evolution of Monogenoidea because we see in this fashion ways of evolution different from the notorious parallelism. It is interesting from this point of view to analyze the Monogenoidea of Selachii within the limits of the primary fauna in connection with separate groups

of parasites with their hosts. In order not to overload the text by excessive enumerations, the data on this question are presented in Fig. 262. From it we can see that each of the families of Amphibdellatidae and Acanthocotylidae is encountered only on one family of Selachii, Loimoidae--on two very close, Microbothriidae--on two very close and one somewhat more removed; whereas Monocotylidae and Hexabothriidae are widely distributed within the limits of the entire group Selachii and are encountered on a vast majority of the families (probably in the future it will be found also on a number of other insufficiently studied families of sharks and skates). At the same time one must draw attention to the distinct difference between the biological peculiarities of both of these last families. Thus, Microcotylidae are worms which move along the body of the host freely; whereas Hexabothriidae at best are capable of small changes of location on a very limited section. If at the same time one takes into consideration that Hexabothriidae are discovered also on Hexanchidae while Microcotylidae are not, one can suppose with a large degree of certainty that the origin of the first is more ancient and that they appeared on Selachii p. 306
earlier than Monocotylidae. Again we shall return to this question later (see page 448).

It is rather easy to characterize the fauna of monogenetic trematodes of the Elasmobranchii and Holocephali as a whole, the one of Teleostomi,on the other hand,can be evaluated only with great difficulty, because the basic mass of all Monogenoidea is on these fishes. Exceptions are formed by groups, already mentioned before, parasitizing Selachii and Holocephali and also the suborder Polypisthocotylinea (order Gyrodactylidea) peculiar only to higher groups of vertebrates (Amphibia and Reptilia). In connection with what has been said, in order to evaluate the characteristic peculiarities of infection on Teleostomi we will have to analyse first the fauna of separate orders of fishes of this class. The data on this subject are reproduced in Table 17.

First of all, the nature of the fauna, of monogenetic trematodes of Acipenseriformes offers interest in connection with the fact that this group is separated into a separate suborder Chondrostei by a large majority of researchers. It is true that L. C. Berg (1940) objects to this, considering that the so-called Chondrostei gradually merge into Holostei and consequently that such a division can be made only artifically. In addition to that, another problem of Acipenseriformes is not without interest. It is a question of their link with Selachii which is now resolved distinctly negatively,whereas A. N. Severtsov (1922a, 1931) considered such links quite probable. At first glance,the considerations of Severtsov expressed in terms of the Monogenoidea are substantiated because representatives of the same order Diclybothriidea are encountered both on Selachii and on the Acipenserids. However, as will be shown later (see page 403), the differences between both families of Diclybothriidea are quite large and they show differences in direction in the general way of regressive development of the attaching apparatus. These peculiarities, namely--the disappearance in one family of a part of the chitinous armature (Hexabothriidae) while it is preserved in the second but with a reduction at the same time of the narrowed part of the disc, convincingly speak for the very ancient divergence of both families. Nevertheless, it remains a fact that both these families are much more related to each other than to the rest of Oligonchoinea.

There are no bases whatsoever to assume that Diclybothriidae chanced upon Acipenseriformes from Selachii secondarily in a relatively recent time. The biology and physiology of the host and the nature of the distribution of Diclybothriidae on them speaks against this. For instance, one can doubt the fact that Diclybothrium armatum has been encountered on Polyodontidae from the time of their separation; it is possible that it transferred to Polyodontidae at a much later time, but there is no basis whatsoever to doubt that this species has been distributed in Acipenseridae from very ancient times and it is much more likely that it passed the entire period of their evolution with them, from the upper Cretaceous at a minimum. Most tempting, however, is the supposition that Diclybothriidae are the descendants of the initial Monogenoidea parasitizing ancestors common for them and for Selachii, that they have an even more ancient history. Only this supposition permits us to understand the reasons for finding Diclybothriidea which are related to each other on fishes which are very distant from each other and the total absence of both on Holostei. In other words, one can suppose that the specialization of Diclybothriidae was already so far advanced at the moment of formation of Holostei that it excluded the possibility of transfer onto the latter.

A completely different picture is offered by the second group of monogenetic trematodes of Acipenseriformes--Capsalidae, among which only one genus Nitzschia is encountered on the fishes which interest us. It is true that it is sharply differentiated from other species and that it forms a special subfamily (see page 382). Nevertheless, the distribution of Capsalidae, about which we have already spoken (page 276,), allows us to maintain that they are phylogenetically secondary parasites of Acipenseridae which appeared on the latter much later than the Diclybothriidae. Taking into consideration that for a number of reasons the White Sturgeon (Huso huso L.) can be considered as the basic host of Nitzschia, it is very probable that the separation of the genus took place historically not earlier than the Pliocene (Berg, 1940). As a result, we can say that the fauna of monogenetic trematodes of Acipenseriformes shows on one hand a sharp differentiation of this group of fishes from the remaining Teleostomi and on the other hand a different chronological sequence in appearance on a given order of both families of parasites which comprise it. p. 307

The fauna of monogenetic trematodes of Clupeiformes indisputably consists of representatives of four families. There are no families of Monogenoidea common for all Clupeiformes and their fauna falls into three groups: parasitizing Clupeoidei (Clupeidae), Salmonoidei (Salmonidae, Thymallidae and Osmeridae), and encountered on Salmonoidei and Esocoidei (Esocidae) at the same time.[1]

The first group consists of representatives of three genera of Mazocraeidae, which are undoubtedly connected with each other in their evolution (see page 419). However, besides these genera, three more (two?--see page 417) genera parasitizing Scombridae pertain to the same family. The close relation of the genera of Mazocraeidae parasitizing Clupeidae and Scombridae does not arouse any doubts and the genera *Mazocraes* and *Octostoma* (Fig. 263) are especially close to each other. The last genus most probably descends from the first or from ancestors very close to it. Thus, this gives us the right to suppose that Mazocraeidae are primarily phylogenetic parasites of the Clupeidae and secondarily for Perciformes. The transfer to the latter is conditioned not by consanguinous relations of the host although they have them but basically by the commonness of ecology of herrings and scombrids and the relatively frequent and constant contact. As is known, during a considerable period of their lives the scombrids feed on young herrings (Nikolski, 1954) and in addition to that they are pelagically gregarious fishes which at younger ages often migrate jointly which was often also observed by us.

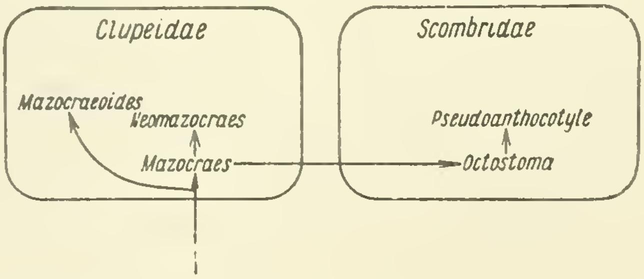

Fig. 263. Diagram of interrelations between the genera of Mazocraeidae and their hosts.

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[1] The data about *Bilaterocotyle* (Protomicrocotylidae) from Chirocentridae are not taken into consideration (see page 228).

The second group characteristic for Salmonoidei consists p. 308
of representatives of the genera *Gyrodactyloides* and *Discocotyle*,[1] i.e., very heterogeneous, for both genera pertain to different subclasses. All species of *Gyrodactyloides* without exception are encountered only on Salmonoidei. As is further indicated, this genus is a derivative of *Gyrodactylus*-like ancestors (see page 399), consequently to speak about the antiquity of its parasitizing the Salmonoidei is very difficult. By origin it is undoubtedly a marine genus, which is confirmed by a number of considerations (Bychowsky and Poljanski, 1953). With its hosts it enters also into fresh waters but it has never been encountered in purely fresh waters on the purely fresh water family of Salmonoidei--Thymallidae. Hence, we can make a more or less definite conclusion about the relatively recent time of separation of *Gyrodactyloides* as an independent genus; for, without any doubt, if this genus had separated before the separation of Thymallidae it would have been peculiar to this family.

The genus *Discocotyle* is widely distributed on Salmonoidae and Thymallidae and is encountered only in fresh water. Just as the remaining genera of Discocotylidae parasitizing Cypriniformes it is a very much altered representative of Mazocraeidae which undoubtedly became adapted secondarily to parasitizing the present group of hosts. More detailed information about the correlations of this genus with others is given somewhat later (see page 311).

The third group peculiar to both the Salmonoidei and Esocoidei consists of representatives of Tetraonchidae and Gyrodactylidae, i.e., it is again different in origin. The only genus of Tetraonchidae, *Tetraonchus*, is characteristic for it; it is encountered exclusively on a number of genera of Salmonidae, on Thymallidae and Esocidae. As regards Gyrodactylidae, in addition to the genus *Gyrodactyloides* indicated earlier, a number of species of *Gyrodactylus* are also encountered on the families of fishes enumerated above (both on Salmonoidei as on Esocoidei). Undoubtedly these are parasites which became secondarily adapted to these fishes. Conversely, one can suppose that *Tetraonchus* is phylogenetically primary for Salmonoidei which then transfered onto Esocoidei. A number of primary (primitive?, *nobis*) traits in the organization of these worms serves as a substantiation of this (see page 388). It is also noteworthy that L. C. Berg groups the hosts into one order--Clupeiformes in contrast to the opinion of the majority of the ichthyologists who separate esocid fishes into a special order of Esocoiformes (Berg, 1940; Nikolsky, 1954). One can consider it as commonly accepted that Esocoidei, which arose at the end of the Cretaceous period, descend from some sort of Salmonoidei (possibly from Osmeridae). Consequently the parasitizing of *Tetraonchus* on both groups independently has a phylogenetically determined character and underscores their indubitable consanguinity; and, it seems to us, forces us to consider the point of view of L. C. Berg as more correct. At the same time, we can suppose that the transfer of *Tetraonchus* to parasitizing Esocoidei is a very old phenomenon because the divergence of contemporary Salmonidae and Esocidae is very great both morphologically and biologically. It seems quite probable to us that this transfer took place in the period of the formation of Esocidae, that is--not later than the Oligocene.

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[1] The indication to the presence of *Encotyllabe* on Salmonidae is not taken into consideration (see page 262).

As a whole the fauna of monogenetic trematodes of Clupeiformes is very heterogeneous and consists of different groups in origin and time of adaptation to present hosts. At that same time we can consider that the phylogenetically primary parasites of the Clupeiformes are, on the one hand, the marine forms--Mazocraeidae, and on the other--the fresh water Tetraonchidae. It is most probable that the p. 309
first family had its origin in the Cretaceous period; whereas the second considerably later, from the Eocene or perhaps Paleocene period.

Up to the present time the actual number of monogenetic trematodes on Scopeliformes is unknown with the exception of one species--*Ancyrocephalus alatus* Chauhan which, as was indicated above, was probably accidentally discovered on these fishes (page 222). Even if one recognizes its origin as normal (natural, regular, *nobis*) then it, without any doubt, chanced upon the present fishes secondarily and rather recently, for its basic hosts are fishes of different orders.

The fauna of Monogenoidea of cypriniform fishes is very considerable in its composition. It is composed of representatives of three orders pertaining to both subclasses.

As is known, the Cypriniformes are basically freshwater fishes. They are divided into two groups which are accepted by Berg, who, however, indicates that it is probable that they represent two separate orders, Cypriniformes (*s. str.*) and Siluriformes. The time of the appearance of these two groups, connected to each other by the presence of the Webberian organ, coincides apparently with the beginning of the Cretaceous period (Nikolsky, 1954).

During the analysis of the fauna of the monogenetic trematodes of Cypriniformes we see first of all that it is very different in its origin and this also pertains to its representatives belonging to the same family. Thus, the fauna of Dactylogyridae is composed of 18 genera, part of which are very numerous; apparently in a number of cases their origin is not linked with each other and thus among the family we encountered both the primary and the secondary, phylogenetically, parasites of Cypriniformes. Attention is attracted to the fact that within the limits of the Cypriniformes all genera of Dactylogyrinae without exception are encountered only on Cyprinidae, Catostomidae, Cobitidae, Characinidae, i.e., only on Cyprini and only in fresh and brackish waters with the single exception of *Dactylogyrus iwanowi* Bychowsky, (see page 110). Without any doubt this subfamily has fresh water origin just as their primary hosts; however, along with the indicated families of fishes, Dactylogyrinae are also encountered on others related to other orders--Perciformes, Anguilliformes, and Gasterosteiformes. Nevertheless, in the cases which serve as examples of the transfer from the primary hosts we deal only with fresh water fishes or the ones which became adapted to life in fresh water. A different situation exists with the representatives of Anchyrocephalinae. Their basic part is also undoubtedly fresh water (as for instance, *nobis*) the genera *Cleidodiscus*, *Urocleidus*, *Pseudomurraytrema*, *Ancylodiscoides*, and *Bychowskyella*, Another small part is known only from marine waters and parasitizes Cypriniformes which became secondarily adapted to life in marine bodies of water and on marine perciformids. Here belongs the genus *Ancylodiscus* parasitizing Plotosidae and Gadopsidae (see page 253). Finally one genus, *Ancyrocephalus*, contains species encountered both on fresh water Cypriniformes (Cyprinidae, Cobitidae) and possibly marine (Ariidae, see page 222 ; *Ancyrocephalus alatus* Chauhan); which, in addition to that, is known from a small number of different orders of marine fishes. As was already indicated, this genus is artificial (see page 264), consequently it is difficult to utilize it for analysis. One can only say about it that its few representatives on Cypriniformes became adapted to parasitizing these fishes secondarily and descend p. 310
from species peculiar to other orders of hosts. As a whole, the Ancyrocephalinae are also encountered on 9 orders of predominantly marine fishes besides the Cypriniformes, consequently the question of their origin cannot be studied only by the analysis of the fauna of Cypriniformes. We shall analyse it in detail later but now, running ahead, we shall only indicate that what seems to us as more probable is the fresh water origin of Anchyrocephalinae, and that at the same time a part of the genera of this subfamily is linked phylogenetically with Cypriniformes primarily and part--secondarily (see page 456). Thus, it is possible to suppose that Dactylogyridae as a whole are primarily

fresh water forms and at the same time, in considerable part, phylogenetically primary parasites of Cypriniformes. However, the fauna of Dactylogyridae of Cypriniformes can be divided into five groups by its structure and links with the hosts. To the first group pertain genera peculiar exclusively to Cyprini--*Dogielius*, *Falciunguis*, *Pseudacolpenteron*, *Paradactylogyrus*, *Pseudomurraytrema*, and *Hamatopeduncularia*. The second group contains genera peculiar basically to Cyprini and discovered on other orders of fishes, but not on Siluri to which pertain *Dactylogyrus*, and *Acolpenteron*. The third group consists of genera basically encountered on other orders of fishes but discovered also on Cyprini and on Siluri--that is *Cleidodiscus*, *Urocleidus*, and *Ancyrocephalus* (see however, page 265).[1] The fourth group is represented by two genera peculiar only to Siluri--*Ancylodiscoides* and *Bychowskyella*. Finally the fifth group consists of one genus--*Ancylodiscus*, encountered on marine Siluri and Perciformes. It is interesting that the third group consists of those three genera about which we have often said that they are artificial (see pages 258-261). With this, if one takes into consideration our analysis of the genus *Urocleidus* (see page 350) one can consider its attribution to the third group as erroneous and its transfer to the second group as more correct, although this also is not quite accurate because it is basically peculiar not to Cyprini, on which it is rather an exception, but to Perciformes. In conclusion, speaking about the fauna of Dactylogyridae of Cypriniformes, we must conclude that actually Cyprini and Siluri each have their dactylogyrid-fauna sharply differing from both groups.

The fauna of Gyrodactylidae of Cypriniformes consists of representatives of two genera of which one is known only from Cobitidae (*Paragyrodactylus*) and a second (*Gyrodactylus*)--besides Cypriniformes from eight more orders and perhaps will also be found on a number of others. There is reason to believe that the genus *Gyrodactylus* is secondarily fresh water although it is very ancient in its origin. It is also probable that the genus *Gyrodactylus* is phylogenetically secondary for Cypriniformes. However, taking into consideration its wide distribution and at the same time the large species specialization one can suppose that its adaptation to Cypriniformes took place almost at the same time as the differentiation of the order itself. As indirect substantiation of this is the noteworthy fact that among the almost 30 species of *Gyrodactylus* known from Cypriniformes, only one was discovered on Siluri and all the rest on Cyprini.

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[1] Apparently *Metahaliotrema* also belongs here.

Discocotylidae from Cypriniformes are again peculiar only to Cyprini and are not known from Siluri. To this family pertain two genera parasitizing Cypriniformes and one of them besides is encountered on Cyprinidae (Diplozoon) and a second, both on Cyprinidae and Catostomidae (Octomactrum). The third genus Discocotyle, which was already mentioned (see page 308) is encountered on Salmonidae and p. 311 apparently is primary or initial or more precisely is closer to the ancestral forms than both genera to the Cypriniformes. Again there is no doubt that the genus Diplozoon is phylogenetically younger than Octomacrum and especially Discocotyle. However, the great specialization of this genus points to the considerable antiquity of its separation. If one takes into consideration what has been said above, one can conclude that this took place not later than the Cretaceous period. If this is so then both genera on Cypriniformes are their initial phylogenetic parasites. At first glance this conclusion stands in distinct contradiction with what has been said about Discocotylidae earlier (see page 308); however, it is not so. Actually we consider that Discocotylidae became adjusted secondarily to existence in fresh water and that they descend from marine Mazocraeidae but at the same time phylogenetically they are primary parasites of Cypriniformes, i.e., their evolution as independent genera began at the same time or simultaneously with the formation of Cyprinidae and Catostomidae.

Finally, Calceostomatidae on Cypriniformes are represented by two genera--Anonchohaptor from Catostomidae and Fredericianella from Ariidae (?, see page 363). Both genera are insufficiently studied and we cannot say anything definite about their links with their hosts, especially since their position in the system is far from being clear to us (see page 362). The only thing that can be said with certainty is that the genera mentioned became adapted to parasitizing fresh water Cypriniformes independently from the remaining Dactylogyridae.

In addition to what has been said before, the analysis of the fauna of Monogenoidea of Cypriniformes leads to the general conclusions about its relative antiquity and a fresh water origin of its greatest part. At the same time, there is reason to believe that the division of Cypriniformes into two separate orders is natural because the data on the distribution on them of monogenetic trematodes confirm the considerable separation of Cyprini from Siluri.

The fauna of Monogenoidea of Anguilliformes is not very large and consists of representatives of two genera of Dactylogyridae and one of Acanthocotylidae.

As regards Dactylogyridae, two species of *Dactylogyrus* are known from Anguillidae and one--of *Ancyrocephalus,* from Muraenidae. Both species of *Dactylogyrus* are known only from eels and it is quite possible that it is the same species (see page 277). In addition, the only species of *Ancyrocephalus* (*A. alatus*, Chauhan) is encountered also on Perciformes and on Cypriniformes. Beyond any doubt the representatives of both genera are recent parasites of Anguilliformes which transferred to them from Cypriniformes (*Dactylogyrus*) and possibly from Perciformes (*Ancyrocephalus*).

The situation is quite different with the only species of Acanthocotylidae--*Enoplocotyle minima* Tagliani. Undoubtedly it is a very primitive species; however, it has certain peculiarities indicating secondary simplifications (see page 385). Inasmuch as all the remaining Acanthocotylidae are encountered exclusively on skates (see, however, page 275) and are, as we have already said, the primary parasites of Selachii it is clear that *Enoplocotyle* transferred to Anguilliformes secondarily; however, as was already indicated (see page 302) in a very remote period. Thus, one can consider *Enoplocotyle* as a characteristic genus only for Anguilliformes and connected for a long time with them in the process of evolution.

Beloniformes have the representatives of four genera--*Ancyrocephalus*, *Axine*, *Neoaxine*, and *Axinoides* in their fauna of Monogenoidea. The first of these genera is represented by two species encountered only on Beloniformes. Undoubtedly these are parasites p. 312
which became adapted secondarily to inhabiting the present fishes and transferred to them in relatively recent times from Perciformes, being in this fashion the phylogenetically secondary parasites of Beloniformes. The genus *Axine*, basically encountered on Beloniformes (on two families Belonidae and Exocoetidae) is known also from Perciformes (see page 256). The genera *Neoaxine* and *Axinoides* are known only from Belonidae. Taking into consideration the secondary nature of the structure of the attaching apparatus of these Microcotylidae, it is most probable that they transferred to parasitizing the family under discussion from Perciformes and this in the relatively recent past. It is noteworthy that in the Perciformes they are encountered only on Carangidae. The latter separated in the Eocene (Belonidae are known from the lower Oligocene; Berg, 1940) just as did the Beloniformes. There are no consanguinous links between both hosts of *Axine* and *Axinoides*. Hence, it is most probable that the transfer of parasitizing from one group of hosts to another was linked by the presence of ecological contacts of both.

The fauna of monogenetic trematodes of Gadiformes is somewhat more diversified than among the preceding orders. Into its composition enter the representatives of two orders of Polyonchoinea and one of Oligonchoinea.

From Dactylogyridae only one monotypic genus--Linguadactyla is known from Molva (Gadidae), This genus is very singular (see page 352), in connection with which it is separated by us into a special subfamily of Dactylogyridae. In contrast to all the remaining representatives of this family it has a number of both primitive and conversely very specialized traits in connection with which its relatively ancient separation from other Dactylogyridae, and apparently very prolonged common existence with the contemporary hosts, does not occasion any doubts.

As regards Gyrodactylidea, a number of species of Gyrodactylus is known on Gadiformes both in marine as in fresh waters [on Lota lota (L.)]. All the species of this genus are strictly specific to their hosts. As was shown by B. E. Bychowsky and J. I. Poljanski (1953), one can maintain for a number of them that they have been connected with their hosts at least from the preglacial period and possibly even from the Paleocene.

Among Oligonchoinea, representatives of Anthocotylidae and Diclidophoridae are known on Gadiformes. In addition, the worms of the first family are known from Perciformes. At the same time there is no doubt that its initial (primary, nobis) species are encountered on Perciformes, whereas the secondarily changed ones are encountered on Gadiformes (see page 427). Besides being on the Gadiformes, the Diclidophoridae are distributed very widely. However, only the genus Diclidophora, which is encountered also only on Macruriformes which are undoubtedly close to them, is characteristic for Gadiformes. As we show later the genus Diclidophora represents a very changed or altered genus (see page 435), and beyond any doubt it descends from forms parasitizing other orders of fishes. The correlations between Diclidophoridae and their hosts will be indicated later in detail (see page 315). On the whole the fauna of Monogenoidea of Gadiformes shows that it is heterogeneous in its origin and is linked by its roots with the corresponding fauna of Perciformes.

As is known, many authors consider that Gadiformes are descendents of common ancestors with Cyprinidae. However, L. C. Berg supposes that such were the forms consanguinous to Pachycormidae and that the Gadiformes arose at the end of the Cretaceous period (Berg, 1940). Also, A. N. Svetovidov is not inclined to consider Gadiformes as being to close to Perciformes, although he points to the fact that the closest relatives of Gadiformes--Macuriformes-- are connected with certain Acanthopterygii (Svetovidov, 1948). p. 313

The fauna of parasites of the closest order--Macruriformes--is very small. It consists only of two genera of Diclidophoridae--*Diclidophora* and *Diclidophoropsis.* Only one species of the first genus is known on Macruriformes, whereas all the rest, as has just been indicated, are encountered on Gadiformes. In contrast to this, two species of *Diclidophoropsis* are known from Macruriformes and Perciformes. On the whole an impression is created that this family of fishes has a fauna of Monogenoidea which links, so to speak, the one of Gadiformes and Perciformes.

It is understandable that the transfer of ancestors of both genera from some families of fishes onto others is very mysterious but it is most probable that *Diclidophoropsis* transferred to Macruriformes from Perciformes and Diclidophora--from Gadiformes, and thus, in spite of the fact that the species of both genera from Macruriformes are independent, the fauna as a whole is secondary. Taking into consideration however, the independence of the species, which has just been pointed out, one must suppose that nevertheless they became adapted to their corresponding fishes a relatively long time ago.

The fauna of monogenetic trematodes of Gasterosteiformes is obviously secondary and consists of one species of *Dactylogyrus* and three species of *Gyrodactylus.* At the same time,if *Dactylogyrus* were obviously acquired in fresh water and beyond doubt represent the descendents of some sort of forms from carp fishes, then on the other hand, the question about *Gyrodactylus* is more complex. Thus, one of the species (*G. arcuatus* Bychowsky) is encountered on purely marine fishes [*Eleginus navaga* (Pallas), *Boreogadus saida* (Lepechin)] it is true in the form of a special subspecies, and is encountered in purely marine regions on sticklebacks. Even though they are discovered basically in fresh waters, two other species were nevertheless often encountered in the sea. Hence, it becomes difficult to speak about the origin of *Gyrodactylus* of Gasterosteiformes.

Four species of Dactylogyridae and two species of Gyrodactylidae are discovered on the Cyprinodontiformes. In both cases they are clearly secondary parasites of Cyprinodontiformes which transferred to parasitizing these fishes from freshwater Perciformes.

Beyond any doubt this transfer did not have any phylogenetic character, and was the result of a constant contact between the representatives of both orders with each other.

For Mugiliformes, the presence of Dactylogyridae, Gyrodactylidae and Microcotylidae is known. On them parasitize the representatives of the genus *Ancyrocephalus* from Dactylogyridae, from Diplectanidae--*Diplectanum*, from Gyrodactylidae--*Gyrodactylus* (on Atherinidae), from Microcotylidae the worms of three genera--*Microcotyle*, *Metamicrocotyle*, and *Diplasiocotyle*, and from Gastrocotylidae--*Chauhanea* (on Sphyraenidae). One can consider that, without exception, the parasites of Mugiliformes are phylogenetically secondary for them, having transferred predominantly from Perciformes (for Mugilidae and Sphyraenidae) and possibly from Cypriniformes (for part of Atherinidae). Inasmuch as Mugiliformes are very close to Perciformes (Suvorov, 1948), this does not occasion any doubt.

Only one species of *Microcotyle* is known on Polynemiformes. It transferred to this group either from Perciformes or perhaps from Mugiliformes, closely related to this order. In both cases the transfer took place relatively recently, because the special species *M. polynemi* MacCallum which is isolated on *Polynemus auratus* is very close to the typical *Microcotyle*.

p. 314 So far only one species of *Gyrodactylus* which transferred, without any doubt, from fresh water Perciformes or, it is even more probable, from Cypriniformes of the far East (Gussew, 1955), is known on Ophiocephaliformes.

The fauna of monogenetic trematodes of Perciformes is the richest. Representatives of 17 families parasitize these fishes,[1] and five of them are not discovered on any other fishes (they are marked in Table 7 by an asterisk). In addition to that, five are discovered on one order of fishes each and seven--on two and more orders. Among the first group there are families containing only one or two genera, narrowly specialized to parasitizing one genus of hosts--they are Tetraonchoididae (see page 394) and Protogyrodactylidae (see page 359). The remaining families have somewhat larger distributions which is apparent from Tables 16 and 17 and also from the corresponding text (see page 265 and further).

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[1] The indication of the finding of Acanthocotylidae on Perciformes is apparently erroneous (see page 275).

It is not possible to doubt that all these five families descend from groups and forms which parasitized the Perciformes also and thus they are all closely connected with the latter from the beginning of their evolution. The five families which are encountered on Perciformes and on one more family (order?, nobis) are apparently phylogenetically also primary parasites of Perciformes. Thus, Calceostomatidae, even though they are encountered also on Cypriniformes, their basic genera--Calceostoma and Calceostomella, beyond any doubt are purely marine in origin and are encountered only on Perciformes. We have already spoken about Dionchidae discovered also on Echineiformes (see page 228 and 256). Anthocotylidae, encountered also on Gadiformes, have primary genera parasitizing Perciformes, which is shown later (see page 426). With only one exception (see page 274) Gastrocotylidae parasitize Perciformes. The exception of this group is formed by Mazocraeidae, which apparently are secondary parasites for Perciformes which transferred to these fishes from Clupeiformes (see pages 307 and 417). As regards the families of Monogenoidea encountered on several orders of fishes, taking into consideration what has been said in the chapters about occurrence of the families and about the system of Monogenoidea, we can say that in contrast to Gyrodactylidae and Dactylogyridae; Capsalidae, Diclidophoridae, Diplectanidae, and Microcotylidae are phylogenetically primary parasites of Perciformes. As regards Acanthocotylidae they are apparently ascribed here erroneously (see page 275). Within the limits of Dactylogyridae the relations are apparently complex. Thus Dactylogyrinae, of which only few representatives of the genera Dactylogyrus and Acolpenteron are encountered on Perciformes, are undoubtedly secondary for the present fishes and transfer to them from Cypriniformes. In contrast to this Ancyrocephalinae are indigenous parasites of Perciformes, and transferred onto other orders from them, as was partially shown earlier. It is characteristic that for the total number of 26 genera, 18 are encountered on Perciformes and in the analysis of independent genera encountered only on other orders it is clearly apparent that the majority of them originates from widely distributed genera of Ancyrocephalinae of Perciformes. An exception is formed by the closely related genera Ancylodiscoides, Hamatopeduncularia, and Bychowskyella which apparently are of very ancient origin and sharply stand out among the rest of Ancyrocephalinae (see page 351). We shall return later (see page 346 and further) to the correlations of the groups within the limits of Dactylogyridae. p. 315

Gyrodactylidae, which are distributed very widely in which they are helped by their very great mobility and the means of infection of the hosts by adult individuals (see page 131), are very poorly studied. Nevertheless, we are inclined to think that their phylogenetic roots are scarcely linked with Perciformes. It is more likely that ancestors of Gyrodactylidae were already encountered in times when Perciformes were not yet separated, i.e., earlier than the upper Cretaceous period.

Capsalidae are biologically similar to Gyrodactylidae thanks to the ability to transfer in the adult state from one fish to another under favorable conditions. They are undoubtedly the primary parasites of Perciformes. Only two subfamilies of the six are not encountered in these fishes. These are the Entobdellinae which will be mentioned later (see page 316) and Nitzschiinae examined earlier (see page 307). As we have already indicated the peculiarity mentioned above allowed Capsalidae to spread widely not only on related but also on very distant groups.

Diclidophoridae are encountered basically on Perciformes. At the same time four genera are peculiar only to them (*Choricotyle*, *Cyclobothrium*, *Pedocotyle*, and *Echinopelma*), one is encountered both on Perciformes and Macruriformes (*Diclidophoropsis*) and two are not peculiar to Perciformes (*Diclidophora* and *Heterobothrium*). Morphological analysis of Diclidophoridae (see page 431) shows that primary forms close to *Diclidophoropsis* which later produced more specialized genera were primary for this group. In this connection, it would have been possible to suppose that the primary Diclidophoridae parasitize Macruriformes; however, this is contradicted by all the data about distribution and morphological peculiarities of the order Mazocraeidae as a whole. Diplectanidae are encountered almost exclusively on Perciformes (6 genera and 33 species from 8 genera and 35 species) and are also their primary parasites. Finally, Microcotylidae indisputably are primary parasites of Perciformes. Of the 15 genera, 12 are encountered in these fishes and only three which clearly descend from the genera encountered on Perciformes, are discovered on fishes of other orders. At the same time a few separated, individualized species of genera peculiar basically to Perciformes became adapted to parasitizing the fishes of other orders. We have already spoken about all these cases (see pages 311 and 313).

As a whole, the fauna of Monogenoidea of Perciformes can be characterized as being very rich and basically linked in its origin with Perciformes with the exception of a few families which became secondarily adapted to parasitizing them (Gyrodactylidae, part of Dactylogyridae and Mazocraeidae). At the same time, the fauna of Monogenoidea of Perciformes gave rise to numerous groups which became distributed on a number of orders of fishes whether linked or not linked with them phylogenetically. In the second case this took place mainly in connection with the peculiarities of the ecology of the hosts (common existence or frequent contact, sometimes alimentary) and certain biological peculiarities of the worms themselves (the ability to move in the adult state and other peculiarities of development).

Dactylopteriformes were obviously studied insufficiently. Only one species--*Parancyrocephaloides daicoci* Yamaguti, is known from them. Taking into consideration the indubitable links between the Dactylopteriformes and Perciformes,one can consider with certainty that *P. diacoci* descends from Dactylogyridae (Ancyrocephalinae) p. 316 of the latter.

Enough has been said before about the fauna of Echeneiformes consisting of representatives of the genus *Dionchus* (Dionchidae). Without any doubt the forms parasitizing the fishes of this order transferred to them from Carangidae secondarily, and one species did not even separate and was preserved as common to Echeneidae and Carangidae [the host records for this species--*Dionchus remorae* (MacCallum) are doubtful, *nobis*].

The fauna of Monogenoidea of Pleuronectiformes is formed of representatives of five families of monogenetic trematodes. Dactylogyridae and Bothitrematidae are represented each by one species only; however, each is quite different in its origin. Thus,*Protancyrocephalus strelkowi* Bychowsky, even though it is specific for flatfishes and even separated on them into an independent genus, is nevertheless undoubtedly a comparatively young parasite of flatfishes and descends from forms which undoubtedly came from Perciformes.

The situation is quite different with *Bothitrema bothi* (MacCallum) which undoubtedly is a very ancient parasite of Pleuronectiformes (see pages 394-397). We are not in a position to say anything definite now about the origin of *Bothitrema.* It is quite possible that it is a very ancient group which separated from the common trunk of Tetraonchidea before the separation of the remaining families except Tetraonchidae.

Apparently Capsalidae parasitizing the Pleuronectiformes are also a very ancient separation. This is substantiated by the fact that Entobdellinae, which are characteristic basically for these species, have a disc apparently deprived of septa (see page 380).

Nevertheless, it is not possible to doubt that the primary forms of Capsalidae of Pleuronectiformes transferred to them from Peiciformes and thus are secondary from the first.

The transfer of a few Gyrodactylidae to Pleuronectiformes undoubtedly took place relatively recently and also undoubtedly from littoral Perciformes.

Finally, Diclidophoridae are represented on Pleuronectiformes by a genus encountered only on them and Tetrodontiformes (Heterobothrium). Again there is no doubt that this genus descends from forms which transferred to these orders of fishes from Perciformes.

Finally the fauna of Monogenoidea of Pleuronectiformes is basically relatively young and with the exception of Bothitrematidae descends from the corresponding one of Perciformes. Inasmuch as the links between Pleuronectiformes and Perciformes are commonly recognized this is quite understandable. The separation of Pleuronectiformes took place approximately in the lower Eocene and even in the beginning of the Paleocene, i.e., considerably after the separation of Perciformes. Hence, it is possible to think that Bothitrematidae and perhaps Entobdellinae separated on Pleuronectiformes also approximately in the Eocene period.

Finally the last order--Tetrodontiformes--has a fauna of Monogenoidea consisting of three genera of Dactylogyridae, two of Capsalidae, and one of Diclidophoridae.

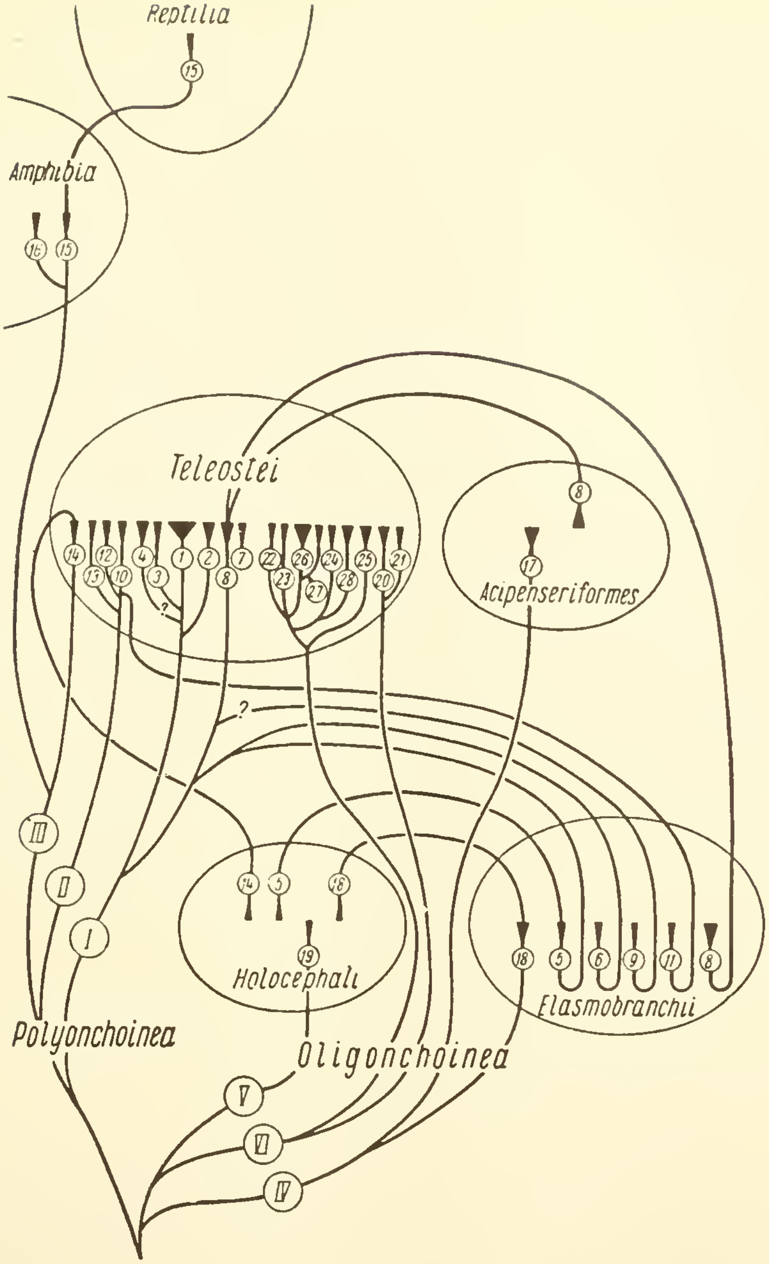
One genus of Dactylogyridae is encountered only on Tetrodontiformes (Ancyrocephaloides), the second--on these fishes and on Perciformes (Diplectanotrema); whereas the third is widely distributed on a number of orders, but basically on Perciformes (Ancyrocephalus). Thus, there is every reason to believe that representatives of this family became adapted to Tetrodontiformes rather recently and transferred to them from Perciformes. The same applies also to Capsalidae which did not form any independent genera nor in- p. 317
dependent species on Tetrodontiformes. Finally, Diclidophoridae are represented by one independent species of Heterobothrium, also descending from forms from Perciformes as has already been indicated.

Hence we can make certain conclusions about a weak individuality of the fauna of Monogenoidea of Tetrodontiformes which separated apparently relatively recently from the one of Perciformes. It is curious that Tetrodontiformes are known from the lower Eocene and perhaps from the upper Cretaceous (Berg, 1947) but nevertheless the fauna of their parasites is much less distinctive than that of Pleuronectiformes.

On the basis of this short analysis of the composition of the fauna of monogenetic trematodes of separate orders of fishes and also of the materials on Amphibia and Reptilia,one can make a number of important conclusions. First of all this pertains to the primary and secondary nature of the links of the parasites with a particular group of their hosts. As a result of the discussion we derived a diagram which gives the idea about the distribution of families of Monogenoidea on large groups of hosts (Figure 264). From this diagram it is apparent that practically speaking the basic large majority of Monogenoidea parasitizes Teleostei with which is linked the flowering not only of the lowest but also the highest Monogenoidea. As regards the remaining groups of hosts, along with the ancient forms which arose during the early stages of phylogenesis of monogenetic trematodes, on them are also encountered species which occur upon them secondarily and which do not change at all on them, i.e., the same as the ones on their basic hosts, or evolving not more than to the degree of an independent species. The exception is formed by parasites of Acipenseriformes--the genus Nitzschia which undoubtedly transferred to the Acipenseriformes secondarily and more likely from Perciformes and,nevertheless, separated not only to the degree of genus but also formed a special subfamily.

What has been said applies to the parasites of fishes. As regards the parasites of Amphibia and Reptilia,here takes place a progressive widening of a circle of hosts beyond the limits of the original hosts--fishes, in connection with which the change of the group bears a different progressive character with the formation of new species, genera,and even with the appearance of new families (Polystomatidae, Sphyranuridae).

Further, in the analysis of contemporary Monogenoidea of separate large groups of hosts we can conclude that between the parasites of these groups there exists a minimal number of transfers which have no phylogenetic significance. Practically, with the faunas of monogenetic trematodes of Holocephali, Elasmobranchii, Acipenseriformes, Teleostei s. str., and Amphibia and Reptilia, each is fully disdistinctive and descends not from each other, but from ancestral fauna which are not preserved. The supposition that these fauna were peculiar to the same groups of hosts and then became extinct on them is unlikely. It is more likely that they were peculiar to the extinct ancestors of the contemporary groups of fishes and that their divergence, apparently very complex in separate cases, took place in the period between the appearance of the primary Monogenoidea and the formation of their contemporary faunas and not groups(!), i.e., during very remote geological times, at any rate not later than the period of formation of the classes of fishes, i.e., not later than the Silurian period.


Reptilia
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Teleostei
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Acipenseriformes
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18
19
Holocephali
18
5
6
9
11
8
Elasmobranchii
Polyonchoinea
Oligonchoinea
V
VI
IV

Fig. 264. The diagram of occurrence of monogenetic trematodes on the basic groups of their hosts. Inverted triangles indicate families primarily parasitizing the given group of hosts, upright triangles--secondarily adapted. Relative width of the base of the triangles shows approximately the volume (number of genera) of the family. The Roman numerals--orders, whereas the Arabics represent families of monogenetic trematodes. I--Dactylogyridea; II--Tetraonchidea; III--Gyrodactylidea; IV--Diclybothriidea; V--Chimaericolidea; VI--Mazocraeidea. 1--Dactylogyridae; 2--Diplectanidae; 3--Protogyrodactylidae; 4--Calceostomatidae; 5--Monocotylidae; 6--Acanthocotylidae; 7--Dionchidae; 8--Capsalidae; 9--Loimoidae; 10--Tetraonchidae; 11--Amphibdellatidae; 12--Tetraonchoididae; 13--Bothitrematidae; 14--Gyrodactylidae; 15--Polystomatidae; 16--Sphyranuridae; 17--Diclybothriidae; 18--Hexabothriidae; 19--Chimaericolidae; 20--Mazocraeidae; 21--Hexostomidae; 22--Anthocotylidae; 23--Discocotylidae; 24--Plectanocotylidae; 25--Diclidophoridae; 26--Microcotylidae; 27--Protomicrocotylidae; 28--Gastrocotylidae.

We will return to the question of the origin of the fauna of Monogenoidea and of their systematic groups (see further), and now we must deal briefly with the data of the nature of the faunas of the monogenetic trematodes of separate orders of Teleostei represented in Figure 265. This diagram represents a further deciphering of the preceding one and gives us a number of important materials explaining p. 319 at the same time, that which has been expressed above. First of all it distinctly shows that a number of orders of fishes does not have its own independent fauna because on them are encountered only separate species of genera of worms characteristic for these orders which have just transferred from the fishes of other orders. In a majority of the cases, however, we deal here with separated independent species which permits us to speak about the beginning of the process of the formation of an independent fauna which at the present time descends from the contemporary fauna of other orders. At the same time, let us note that when we speak about contemporary faunas we mean, of course, not the present historical moment but the Quarternary period and in separate cases perhaps even the end of the Tertiary. To the orders of fishes having precisely such faunas one should ascribe Echineiformes, Polynemiformes, Macruriformes, Ophiocephaliformes, Cyprinodontiformes, Gasterosteiformes and Scopeliformes, i. e., 7 of 17 orders of Teleostei,[1] on which monogenetic trematodes were discovered. Thus, only 10 orders have their own independent faunas and the relations here within the limits of separate orders are quite different. Thus, the faunas of Monogenoidea of Beloniformes, Mugiliformes, Dactylopteriformes, Anguilliformes and Tetrodontiformes, even though they contain independent genera and in some cases there are several of them, are nevertheless secondary, deriving from the fauna peculiar to Perciformes and becoming independent in this fashion also relatively early, it is true more likely at a more ancient time than the faunas of the first seven orders. The situation is different with the other five orders. Along with the groups which transferred to them from other orders of Teleostei, they contain also the groups of different taxonomic significance appearing on them primarily, which is clearly visible from the diagram under study. At the same time, two orders, Pleuronectiformes and Gadiformes, basically have faunas which clearly transferred to them from the Perciformes and only an insignificant number of species is primary for the given fishes.

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[1] Excepting Acipenseriformes.

The transfer of these species took place probably from some forms of extinct groups of hosts at the very beginning of the formation of Pleuronectiformes and Gadiformes. The Clupeiformes, which have ancient forms of parasites of both subclasses, are distinguished by a much more original fauna. However, as a whole the fauna of Clupeiformes is nevertheless relatively poor. Practically only two, it is true the most numerous orders--Perciformes and Cypriniformes, are characterized by a large distinct fauna. Attention is attracted by the fact that one of their orders is basically marine whereas the second one of these orders is almost completely fresh water. The existing exchange by the separate groups of Monogenoidea between these two orders is clearly secondary and only underscores the possibility of transfer in certain conditions (limited or confined conditions, *nobis*) of fresh bodies of water. The distinctiveness of the fauna of the three largest orders of Teleostei shows undoubtedly not only the plurality of the possible "ecological niches" but also the relative antiquity of these faunas. It is impossible not to note that all these three orders of fishes originate approximately at the same time because their fossil remnants begin to be encountered at the same period--in the Cretaceous period.[2] It is understandable that the Clupeiformes are somewhat more ancient than the two remaining orders especially since the origin of Perciformes is even linked with Clupeiformes (Suvorov, p. 320 1948). Hence we can conclude that the beginning of the development of the faunas of parasites of these three orders can also be supposed as linked either with the Cretaceous period or with a somewhat earlier period, That is much later than the origin of the fauna of the examined groups of hosts.

A general preliminary conclusion from the examination of the faunas of monogenetic trematodes of different groups of their hosts can be that in the analysis of phylogenetic relations of separate groups of Monogenoidea in addition to the evaluation of their own interrelations the inspection of the nature of the origin of separate groups is also indispensable. The application of such inspection will give clear notions about the general progress of evolution.

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[2] Clupeiformes are known from the upper middle Triassic, whereas Clupeoidei--only from the lower Cretaceous, and Salmonoidei--even from the lower Eocene. Cypriniformes are known from the upper Crateceous just as are the Perciformes.

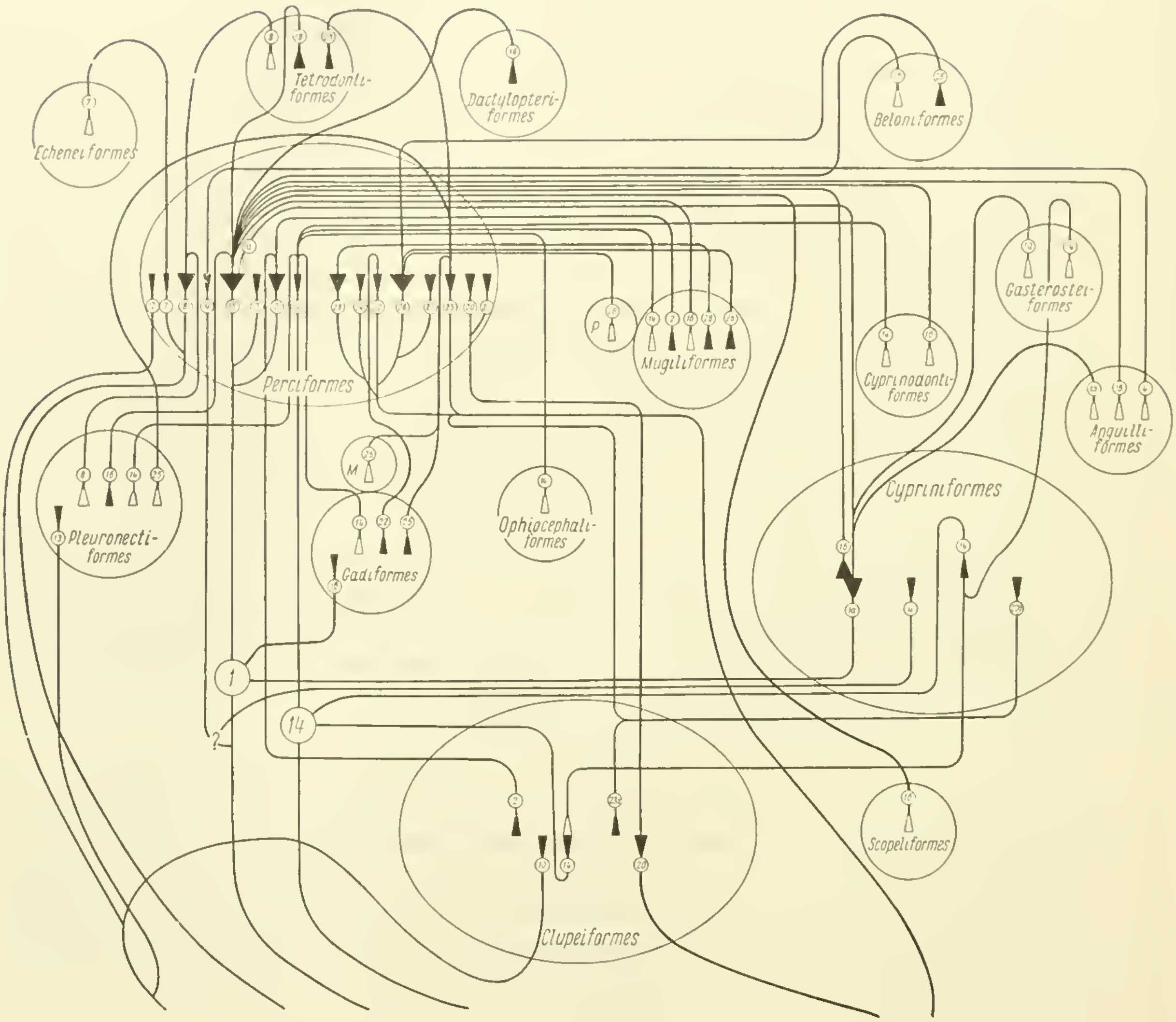
Echeneiformes
Tetrodontiformes
Dactylopteriformes
Beloniformes
Perciformes
P
Mugiliformes
Gasterosteiformes
Cyprinodontiformes
Anguilliformes
Cypriniformes
Pleuronectiformes
M
Gadiformes
Ophiocephaliformes
1
14
?
Scopeliformes
Clupeiformes

Fig. 265. Diagram of occurrence of monogenetic trematodes on the orders of body fishes. The designations are the same as in Diagram 264. In addition to that the dark triangles signify that in the given group of hosts occur parasitic worms which are separated at least to a degree of independent genera, whereas the white triangles--that in the given case takes place the occurrence of species pertaining to the genera characteristic for another order of fishes. 1a--Dactylogyrinae, 1b--Ancyrocephalinae, 1c--Linguadactylina 23a--Discocotylinae, 23b--Diplozooninae (basically and partially Discocotylinae); M.--Macruriformes; P.--Polynemiformes.

PART III

SYSTEMATICS AND PHYLOGENY OF MONOGENETIC TREMATODES

Page Numbers In Margins Refer To Original Russian Text

PART III

SYSTEMATICS AND PHYLOGENY OF MONOGENETIC TREMATODES

CHAPTER 1

BASIC DIRECTIONS OF PHYLOGENY OF MONOGENETIC TREMATODES

In considerations of the phylogeny of monogenetic trematodes we p. 323 must first of all bear in mind that all our constructions are based only on indirect data, for paleontological remnants of these worms are unknown. In order to reconstruct the phylogeny we must utilize the information of the data of comparative anatomy, on the postembryonal development of worms and finally, as we attempted to show earlier, the data on their occurrence, In addition, the latter can to a certain measure, if not replace them,at any rate, reflect paleontological materials, because even though it is not quite complete nevertheless considerable information on paleontology of the hosts exists. One cannot fail to note that we can apply also our data on life cycles to the construction of phylogenetic schemes because the nature of the latter shows that the existence of parasites and hosts which finds its reflection in the complexity and "tight-fitness" (closely coordinated character, nobis) of their life cycles, bear a very ancient nature in a number of cases.

We suppose that the presence of materials on all the sections which we have indicated allows us, in the re-creation of the history of the development of the group as a whole, to consider that the schemes obtained by us reflect accurately the process which took place in actuality. Completely understandable and possible errors will pertain mainly to individual details and not to the general direction and basic lines of development.

Although D. M. Fedotov (1938) objected to our schemes published in the work of 1937, considering as inadmissible the representations of the schemes in time without the presence of paleontological material on the given group, we completely disagree with him. The data on the paleontology of the hosts plus the analysis of the relations of the latter with the parasites living on them allow us to tie the stages of development of monogenetic trematodes to specific historical periods with a sufficient degree of probability. In our research we widely employ the generalizations of V. A. Dogiel about oligomerization and poly-

merization of the organs and of their role in the evolutionary processes of the animals. It seems to us that the ideas of V. A. Dogiel are very fruitful and must always be kept in sight during phylogenetic research. Similarly, in a number of cases it is indispensable to remember and to use the consideration of V. N. Beklemishev about the importance of the basic plan of the structure of the animals. General architectonics and its study undoubtedly play an important role in any phylogenetic research. Finally, as we will see later, one must not forget also the teaching of A. N. Severtsov about the way of evolution which often gave the key to the understanding of general directions of evolutionary process p. 324
in a given concrete group.

Let us now pass to the direct exposition of the basic consideration about evolution of monogenetic trematodes and, without touching upon the question of the origin of the group as a whole, to which a separate chapter is dedicated, make an attempt to re-establish the structure of the primary, the most primitive monogenetic trematodes and the original ways of their development.

In the chapter about individual development of monogenetic trematodes, we already indicated on the basis of the structure of the larvae of contemporary species that the primary form could have the structure represented in Fig. 115. Let us dwell somewhat more in detail on the morphology and other peculiarities of this hypothetical form. As was indicated in the chapter on occurrence (see page 291), as the first monogenetic trematodes can be considered forms which differ from the straight-intestined (Rhabdocoela nobis) Turbellaria both by means of alimentation and by way of morphological adaptations to the constantly moving attachment on the body of the host. These morphological adaptations, characteristic for the present evolving group, undoubtedly were chitinous attaching formations (see page 96). They undoubtedly were not new formations but derived by way of the change of some sort of skin-thorns of Turbellaria.

Apparently the primary armature of monogenetic trematodes had the shape of small thorns lying on the ventral side and undoubtedly predominantly on the posterior end of the body. The latter was connected with the fact that during the process of feeding on the coverings of the body of the host the anterior end of the parasite had to have the ability for quick movements (locomotion), and by this very fact its fixation had to be achieved by contrivances other than the thorns which, with their considerable number and weakly developed nervous system, could hardly have easily acted in a co-ordinated fashion. This is confirmed by the study of contemporary forms. With the significant number of chitinous attaching formations located thereon, the locomotion of the posterior end is either hampered or practically completely impossible. As regards the anterior end, its attachment and disengagement takes place very easily and very quickly for, during feeding the worms usually move their cephalic ends very quickly, attaching them only for a short time during the seizure of the food.

Thus, the body of the primary monogenetic trematodes was differentiated into functionally and morphologically different sections--the anterior end which played a role in alimentation and the posterior served for the fixation of the animal to the body of the host. At the same time the posterior end, in addition to the chitinous armature, also retained a number of agglutinating glands which is observed among many contemporary forms.

As regards the anterior end, its attachment among primary forms took place apparently with the help of unicellular glands located along the anterior end of the body in a more or less wide band analogous to the lobe glands of the Turbellaria.

The coverings of promonogenetic trematodes most probably were represented by a ciliary epithelium; however, the nature of its distribution is not completely clear. Taking into consideration that a process of reduction of the ciliary covering, mainly by way of its disappearance on the dorsal side (often among the oldest ages), is observed among a number of Turbellaria (Beklemishev, 1937) one can suppose that among the original forms of monogenetic trematodes the ciliary epithelium was also rarified on the dorsal side and had the tendency toward the formation of separate ciliary zones. At any rate it is quite probable that the contemporary, very specialized covering of monogenetic trematodes appeared gradually and did not exist among the original forms. p. 325

The internal organization of promonogenetic trematodes can be characterized fairly accurately. The digestive system was represented by a buccal opening lying near the middle of the body, by a sufficiently powerful pharynx of the type pharynx-plicatus and by a sac-shaped intestine. Digestion took place by means of phagocytosis similar to that which takes place among the majority of Turbellaria and all the lowest Monogenoidea. The excretory system apparently did not differ in any way from the one of the contemporary forms with the exception perhaps of its greater simplicity. The structure of the excretory system of the larvae of monogenetic trematodes and its structure in a majority of Turbellaria and particularly among Rhabdocoela serve as the basis for such a conclusion. However, it is difficult to say, judging by the large numbers of the trunks of the excretory system of Diplozoon and of certain other Monogenoidea, whether the presence of the ciliary covering is a primary or secondary phenomenon. It is possible that the original monogenetic trematodes possessed not only clearly expressed terminal nephridial cells but also undifferentiated ciliary covering in the region of the excretory vessels.

The nervous system of promonogenetic trematodes was constructed along the type peculiar to the majority of Rhabdocoela and which was preserved also among the lowest Monogenoidea. Characteristic for it is the presence of a more or less well-developed cephalic brain with three pairs of nerve trunks departing posteriorly from it of which it is possible that the most highly developed were the ventral ones. It is most probable that already during the early stages of the separation of the group, the ventral nerve trunks formed small gangliar thickenings in the posterior part of the body which served to control the attaching armature. The organs of feeling were represented by dermal sensory terminals and undoubtedly by eyes. The latter apparently existed in a small number from the very beginning. Most probably there were two pairs of them, just as is observed among the majority of the lowest Monogenoidea. It is interesting to note that the majority of contemporary Rhabdocoela have one pair of eyes, which points to a greater primitiveness of the primary monogenetic trematodes in this respect.

Finally, the sex system of the latter most probably was similar to the one of the contemporary Dactylogyridae. There is no doubt that at first the promonogenetic trematodes had only one testis and not two as is supposed by Fuhrmann (see page 55). All the lowest monogenetic trematodes, without exception, have a single testis and its division into a greater number of separate parts is beyond any doubt a secondary phenomenon which is observed independently in a number of groups of monogenetic trematodes. This is a very important difference between monogenetic trematodes and Rhabdocoela[1], which usually have two testes and only in rare cases one. Just as for Turbellaria, the presence of separated envelopes of the testes and of individual walls in the seminal ducts is characteristic for the primary forms of monogenetic trematodes. One must suppose that the primary forms already possessed the chitinous armature of the male sex system. The female sex system is represented by one compact ovary,[1] and vitellaria and p. 326

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[1] and also of digenetic trematodes!

[1] This, however, can be untrue--see page 475.

more or less simple effering ducts, consisting most probably of a single oötype opening exteriorly by an independent (as regards the male sex system) aperture.

Such are the basic traits of the primary monogenetic trematodes reconstructed on the basis of the data of the structure of contemporary larval and adult monogenetic trematodes. If we compare this hypothetical form with contemporary Turbellaria we shall see its unusual similarity with a number of Rhabdocoela--Dalyellidae.

As was already indicated (page 291) apparently the primary forms had a wide specificity and were encountered on the body surfaces of their hosts. At the same time their life cycle was completely primitive, i.e., the differences between the structure of the larva and the adult animal were minimal. Maturity was reached in a very short period and the sex system functioned either during the entire year or in its warmest period, i.e., it was limited mainly by the temperature regime and not by the life cycle of the host.[2]

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[2] Hence the above-mentioned supposition about the presence of only the oötype, for the absence of the uterus is characteristic for forms with a continuous or extended period of egg-laying and not the apportioned one.

Further biological process of the development of the group took place by way of greater narrowing of the degree of specificity and the greater adaptation to parasitizing special sections of the body of the host and of timing to the life cycle of the host, i.e., the concentration of reproduction with a certain period and of the working out of corresponding types of morphophysiological structures and peculiarities. However, this progress did not proceed in one general direction but several, reflecting the specificity of different peculiarities of the morphology of the groups of hosts, the direction of the joint existence of a given pair of species of parasite and host and those concrete conditions of the medium in which the host lived. The latter are reflected in its biology, through it--on the parasite and they also influence the latter directly.

At the same time one must bear in mind the eight variants of possible historical interrelations of the species of the parasite and the host, about which we have already spoken (see page 298).

The gill cavity of the fishes can indisputably be considered as the initial (and basic or chief, nobis) place of habitation of monogenetic trematodes.[3] This is fully understandable, because with the relatively weak attaching capabilities of the primary (ancestral, nobis) forms the possibility of survival was greater in the given place where the fortuitous disengagement of the animal does not entail certain loss of connection with the host, and the chances for secondary attachment are considerable. However, the conditions of the gill cavity are not homogeneous and we see that there are two basic directions of adaptations to existence in it; the first is the working out of peculiarities which permit parasitizing the internal surfaces of the cavity, and the second, parasitizing directly on the very gills, mainly the gill filaments. Although there are considerable differences between both places of habitation, the initial stages of adaptation to both apparently were similar and the divergence in the working out of the morphological peculiarities took place much later. One can note one more charac- p. 327
teristic peculiarity apparently connected with the conditions of feeding on both basic places of habitation, namely, that in parasitizing on the flat surfaces (interior surface of the gill cavity) the worms retain the ability to move, whereas on the gill filaments they practically lose it very quickly.

In connection with this, we see that in the adaptation to parasitizing on the flat surfaces, the body of the animals gradually changes from the elongated, terete shape to the flattened, leaf shape. At the same time, the change in the organs of attachment takes place by way of the gradual functional replacement of chitinous formations by muscular suckers which impart greater possibilities of increasing the ability of the worm to attach while maintaining its ability for quick disengagement. The peculiarities of feeding of the forms of this line of evolution of monogenetic trematodes apparently demands the moving of the body of the animal during feeding and, because of the fact that the animals move like leeches, greater or more powerful attaching formations appear on the anterior end of the body, but again changing in a definite direction from the glandular border toward the glandular sucker type and then to the purely suction organs of the type of the suckers of digenetic trematodes. As regards the internal organization of the worms, here also takes place a number of changes connected with the same way of adaptation. Thus, with the greater development of the attaching disc and its parts the nervous system also forms a more powerful nerve ring in it with strongly developed ganglia which are almost equal in sizes to the cephalic ones. Further the flattening of the body and its relative increase leads to the powerful development of the digestive system,forming numerous lateral outgrowths and many different anastomoses between the trunks. Finally,the sex system also undergoes certain changes, particularly in many species the aperture of the uterus begins to be displaced towards the side of the body which facilitates egg laying independently of the position of the body of the worm.

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[3] This does not contradict the location on the surface of the body indicated above for monogenetic trematodes.

In a majority of the cases the animals which became adapted to existence directly on the gills retain their cylindrical bodies and the development of the attaching organs proceeds by way of the increase of the chitinous armature mainly in the form of the increase in the number and complication of the separate parts of the attaching apparatus. This, in the final analysis,leads to the motionless form of life in spite of the fact that either of the parts of the attaching apparatus can by itself attach or detach from the body of the host. In connection with the sedentary way of life the anterior part of the body does not need powerful attaching formations, but,inasmuch as fixation of the anterior end during feeding is indispensable (see page 81),special sucker-shaped formations also develop in the species of this line of evolution, formations which often lie directly in the buccal cavity. The increase in the dimensions of the body leads, in parallel fashion to what we saw in the preceding line, toward the same changes in the structure of the intestines, that is to an increase in the number of outgrowths extending into all parts of the animal. As regards the sex system,its changes already bear a more special nature, even though it is related to the peculiarities of the attachment of the animals, but without any definite tendency.

What has been said above about the two basic directions of the evolutionary process among monogenetic trematodes gives us a basis for a casual analysis of the morphophysiological changes taking place in concrete phylogenetic stages and makes it possible for us to evaluate the significance of changes of different morphological characteristics.

As is evident in the evaluations of ways of evolution we attach special significance to the method of attachment of monogenetic trematodes to their hosts, considering it to be a leading adaptation determining the process of the evolution of the group. However, it does not mean at all that one can utilize only these characteristics for the classification of the phylogeny of the group but, just as we attempted to note and as we shall show further on, the concrete material of the systems of attaching formations undoubtedly gives us the possibility for p. 328

a very accurate understanding of correlations between the separate groups of monogenetic trematodes. At the same time, we must keep in mind that the attaching formations of monogenetic trematodes represents a complex system with a different degree of integration, consequently it is completely unjustifiable to equate the system to one characteristic alone. It will be more correct to evaluate them as a complex of characteristics linked correlatively with each other.

In the chapter about individual development we have already spoken (see page 99) about the tendencies and directions of the change in the attaching apparatus, however, it is indispensable to return to this question.

As a study of the development of contemporary monogenetic trematodes shows, there are two basic types of larvae of which generally each is typical for one of the indicated basic ways of evolution of the group, although the beginning stages of these ways are characterized by adaptations to parasitizing the gills directly and begin to differentiate themselves only later. This undoubtedly points to the great antiquity of this way of development with a sufficient antiquity of separation, of both ways because the larvae themselves are adapted to the free form of life, but reflect by their morphological differences hereditarily consolidated tendencies to the subsequent direction of the morphophysiological evolution.

At the same time we see that in both groups of larvae and correspondingly in adult forms the changes in homologous and nonhomologous organs and formations take place in parallel fashion and independently of each other. The reasons and circumstances connected with this will be discussed by us later (page 464).

Let us pause on the attaching armature of the worms of the line of development of the monogenetic trematodes characterized by the larva of the first type.

As we saw in the re-creation of the promonogenetic trematodes, the latter apparently possessed numerous undifferentiated attaching thorns which were possibly curved into a hook shape from the very beginning of the formation of the group. Further process went along the line of their qualitative change--morphological complication and "improvement" [from the point of view of their adaptation to the basic (chief, nobis) new function--attachment] and a quantitative--initially only of decrease and then increase in the number of new chitinous formations on the new bases (foundations, nobis) at the expense of (in the shape of, nobis) new chitinous formations which were analogous to the first. As we shall see, the latter is not quite clear.

The quantitative changes of the primary undifferentiated thorns proceeded along the line of their adaptations to the best attachment to the body of the host and the simultaneous possibility of a relatively easy detachment, i.e., toward the formation of hooks equipped with musculature and not of constantly acting hook--anchors, similar, let us say, to the ones on the proboscis of Acanthocephala and of the scolex of tapeworms and so forth. The nature of separate ways of concrete changes will be discussed later during the examination of the systematics of monogenetic trematodes, but for the time being we shall indicate that the morphology of a fully developed edge hook of mono- p. 329 genetic trematodes--homologous to the primary chitinous thorns (see page 28), shows that it is completely adapted to the fulfillment of the function indicated above. At the same time we must not forget that the edge hook is not an isolated formation: it, together with the adjoining part of the attaching disc and with the corresponding musculature, represents a complex organ apparently equipped also with a special innervation. The basic direction of change of the edge hooks is clear, it is a differentiation in the hook itself (hooked part, nobis) used for the penetration into the tissue of the host, and in the offshoot which serves as a stop during its fastening and, which is most important, during its removal, and finally in the handle, which serves for the attachment of the basic muscles and also as a stem for the supporting of the part of the disc during the attachment of the hook to avoid sliding and to result in a greater contact between the disc of the parasite and the body of the host. Along with this qualitatively new phenomenon appears the phenomenon of the so-called middle hooks which have a different structure (see page 28) and correspondingly also another method of action, although their physiological significance is analogous to the one of edge hooks. Apparently, within the limits of the first way of evolution, the middle hooks as a rule are new formations and are not formed at the expense of altered edge hooks (are not merely modifications of edge hooks, nobis). The basic line of their development is the increase in strength (not in size, but in function) by way of greater and greater development of both extensions serving for the attachment of muscular bands and also for articulation again with new formations, the connecting plates, which appear as a rule only in the presence of the chitinous hooked armature. The integration along the line of the formation of the system of all middle hooks, middle plates, and muscular and tendon bands is characteristic for middle hooks, whereas each of the edge hooks forms a system which acts independently although generally in concord with each other (however, not always!).

The coordinated action of the system of the middle hooks with a part (predominantly two) of the edge hooks can be considered as the highest degree in integration in the action of the chitinous hook apparatus.

As regards the quantitative relations, the gradual decrease from the initially considerable number to the eight, seven, six, and five pairs of hooks encountered among contemporary species is characteristic for the edge hooks. At the same time the reverse process is characteristic for the middle hooks--increase of their number from one to two or three pairs. However, one must stipulate that among the contemporary forms the absence of middle hooks is a predominantly secondary phenomenon (see Bychowsky and Gussew, 1955 and page 347).

One can consider that in the general branch of monogenetic trematodes which have the larvae of the first type, there are different smaller directions of evolution which differ in the nature and direction of the evolution of the attaching apparatus. As the most primitive, but at the present time represented by a large number of species, we can consider the direction in which the attachment of the animals to the body of the host takes place only by means of the chitinous armature in all phases of the life cycle (except of course the free-swimming). The second direction of evolution within the limits of the first branch of monogenetic trematodes can be considered the way of adaptation for the attachment to the body of the host during the gradual and historically functional replacement of the chitinous armature directly by the p. 330
attaching disc itself during the life cycle. At the same time, during the early stages of the life cycle, and also the more historically ancient species (and among the contemporary morphologically more primitive), the worms attach themselves by means of the same chitinous apparatus (which is subordinated, in the beginning, to the same morphological principles) and then in later stages the attaching disc, changing more and more, transfers into a more or less powerful sucker, completely assuming the function of attachment. The increase of the attaching power of the disc-sucker is reached by two ways which often proceed in parallel fashion and at the same time; namely, by means of a greater and greater development of its musculature (and at the same time the musculature of the suckers is not smooth at all, but transversly striated--the functional meaning of this is not fully clear considering the nature of the action of the attaching organs of the present group), or (and) by way of increasing the power of the sucker by the formation in it of a number of partitions--septa, which increase the volume of the sucking surfaces. As regards the chitinous hooked apparatus, among more highly organized forms it loses its functional significance during the very early stages of development almost completely; whereas among separate forms the middle hooks begin early to degenerate and perhaps even disappear partially or completely.

As a similar direction of evolution connected with the way indicated is the adaptation toward the attachment by means of suckers formed on the attaching disc and functionally replacing both the chitinous armature (playing the role during the early stages of the life cycle) and "the attaching properties" of the disc itself. It would have been tempting to visualize the formation of such a type of attachment as a subsequent stage of development of the disc-sucker equipped with separate suction pits which arise as a result of the separation of the disc by septa; however, this is not true. The fact that the suckers of the disc represent new formations is confirmed easily by the fact that the type of their inception at the place of the edge hooks (see page 185) does not correspond to the formation of the suction pits on the disc-sucker, which are incepted toward the center from the edge hooks. Thus, it is a special line of evolution connected, as a matter of fact, as is known to us, with the change to parasitizing the new group of hosts, Amphibia and Reptilia. However, the same type of new formation is also characteristic for one very old group of monogenetic trematodes, Hexabothriidae, pertaining to another trunk of development of Monogenoidea.

One more branch of the first line where Acanthocotylidae belong is characterized by a special type of development of the attaching apparatus. About it one should only say now that here the primary disc with the typical chitinous armature is functionally replaced by an attaching disc which is formed completely anew. As a matter of fact, more in detail will be said later about this line of evolution (see pages 383 and 456).

In conclusion, within the limits of the first trunk of monogenetic trematodes we see four basic directions of which the first three comprise a huge (in relation to the over-all) number of very diversified species. Let us not forget that for the time being we are speaking only about the ways of evolution of the attaching apparatus, but whether or not they correspond basically to the ways of evolution of the monogenetic trematodes as a whole must be subjected to further discussion.

Within the limits of the monogenetic trematodes which are characterized by the larva of the second type (see page 100), the basic lines of development are considerably more homogeneous. One can p. 331
consider that the larval hooked armature, in principle very close to that of the first type, functions during the early stages of development and then for the entire group as a whole its replacement by new formations--clamps, (see page 161) or a combination of a clamp and a sucker united together with a prevailing action of either a chitinous clamp or a muscular sucker, is characteristic. One cannot fail to note that among almost all species pertaining here the chitinous hooked armature loses its significance earlier and earlier so that the separate forms are even partially deprived of it already in the free-swimming larval stage (see page 201). As regards

the clamps and the clamp-suckers formed anew, they are located not only on the primary attaching disc but also on the sections of the body of the animal lying above it, which are often not even separated from its basic part.

Thus, the second trunk of the development of monogenetic trematodes is much more homogeneous in the sense of a general direction of the evolutionary development of the attaching apparatus,

However, examining the nature and the direction of evolutionary changes within the limits of the given type of attaching armature we can note a number of important tendencies of both qualitative and quantitative nature.

The qualitative changes observed in the given type of development are reduced to the gradual complication of the initially simply-formed clamp (see page 32), both by way of the increase in the number of separate chitinous parts with the preservation of the basic plan of the typical clamp, and by way of the growing together of the separate parts and of forming a complex capsule for the movably-joined halves. At the same time, we also observe the separation of the clamp proper from the sucker, and this process proceeds in the direction of the complete disappearance of the clamp of the sucker which is separated inside in the beginning. Finally, one often observed the differentiation in the sizes of the clamps and one large pair assumes the basic function of the attachment of the animal (Bychowsky and Nagibina, 1954). The qualitative alterations proceed in the direction of an increase in the number of attaching clamps, but the reverse process apparently also plays a role in separate cases (page 442). Among species with a considerable number of clamps, attention is drawn to the fact that the latter are different in origin in spite of their complete morphological similarity. Thus, the first four pairs of the clamps are formed on the base of the initial or primary hooked apparatus, whereas the subsequent ones represent new formations (see Dogiel, 1954a and also page 161). Also important is the tendency toward disruption of the asymmetry of the attaching formations by way of the unequal number of the inceptions of the attaching clamps on each side of the body at the time of their individual development. This phenomenon practically leads to a different asymmetry of the animals and this process can proceed differently (see page 442). No such type of evolution is observed within the limits of the first trunk of monogenetic trematodes. This peculiarity, encountered in the second type, underlines the circumstance that here generally takes place the process of autonomization of separate parts of the attaching apparatus in contrast to greater and greater integration noted within the limits of the first type.

Thus, summarizing what has been said before, we can see that within the limits of both groups of monogenetic trematodes characterized by different types of larvae, basically there are three (or four) main directions of evolution of the attaching organ. If one should analyze p. 332 again the changes in other systems of organs, examining them within the limits of each of the groups cited, he will see that a number of peculiarities in all groups changes quite normally and similarly within the limits of each of the groups. Thus, the digestive system becomes more complex and increases in relative size by way of the growth of the lateral diverticulae and of internal commisures in the direction from the more simple, among the species (of smaller sizes) with more primitive armature, to more complex among species (more often of larger sizes) with a complex system of attaching organs. At the same time, however, this tendency cannot be attributed to the increase in the size of the body because in a number of cases the species with the more complex attaching apparatus have also a more well-developed digestive system even though they have the same body sizes. Thus, for instance, the representatives of the genus *Ancyrocotyle* have a more simple attaching armature and a simple unbranching intestinal tract whereas *Megalocotyle* or *Macrophyllida*, which are approximately of the same size, possess a more complex armature and intestinal trunks with numerous lateral outgrowths. Within the limits of all groups the attachment of the anterior end takes place by means of the secretions of the cephalic glands among species with the more primitive attaching apparatus, and, during further complication, the change in the beginning proceeds toward the direction of the concentration of the glands and then their replacement by muscular formations of the sucker-type. It is understandable that there is no absolute convergency but the parallelism of the tendency is very distinct. Thus, within the limits of the first direction of evolution the process reaches maximal concentration of cephalic glands, in the second direction--to the formation of two cephalic suckers and in the third--one sucker and in the fourth--the appearance of two suckers inside the buccal cavity.

Because of the fact that the excretory system is poorly studied it is difficult to speak about its changes, however, its complication apparently develops concurrently with the complication of the digestive system and with the general growth of the dimensions of the body. The changes in the nervous system bear the character of its greater concentration and, as has already been indicated (see pages 50 and 327), the increase in the development of ganglia in the posterior part of the body in proportion to the complication of the attaching armature. The given process is more sharply expressed in the first three lines, in connection with the peculiarities of the development of the attaching apparatus indicated above for the first trunk in comparison with the second (see page 328).

Finally, the sex system shows a number of parallel changes in all groups. Thus, within the limits of each group, the testes have a tendency toward the increase in number from one to several or to the formation of a large follicular mass about which it is impossible to say whether it represents a single or a multiple organ (see Dogiel, 1954a, and also page 57). Parallel to this, in the majority of the cases the formation of the seminal reservoirs and generally the complication and elongation of the male sex ducts also takes place. The female sex system also has a tendency towards increasing in size and toward complication of the shape of the ovary, and the latter begins more and more to separate sharply into two parts--one containing oögonia and one containing formed oöcytes. As a rule the ducts of the female system become complicated and the appearance of the ductus genito-intestinalis is very characteristic among more highly organized groups (as we suppose in parallel fashion and independently in Polystomatidae and Oligonchoinea, see pages 398-402). Finally one cannot fail to note that the appearance and development of the uterus also takes place in parallel fashion in all groups which were noted.

At the same time we see also the changes of the biology of the animals in the direction of the complication of their life cycle and of its greater and greater adaptation to the life cycle of the host (see page 128). It is understandable that numerous morphological changes, and in the first place--changes of the sex system, are closely connected and depend on the change of the life cycle, reflecting the peculiarities of new physiological adaptations. p. 333

In conclusion, we suppose that in the formulation of the system of monogenetic trematodes reflecting the phylogenetic relations, it is indispensable, first of all, to pay attention to the attaching apparatus as a leading adaptation characterizing a given group, taking into consideration the changes in other organ systems. Possible objections and attempts to build the system on the basis of other characteristics are not justifiable and do not reflect true relations within the limits of the group. This is convincingly substantiated by the coincidence of the materials on the directions of development of the larvae and the tendencies of the development of adult monogenetic trematodes which have just been expressed. From all that has been said it is clear that in the attempt to build a system on the basis of only the characteristics and tendencies in the development of the sex system, let us say, we will obtain only an artificial unification or joining of species completely different in origin which have only a converging similarity (which can be easily proven by the structure of the attaching apparatus).

In this connection, one cannot refuse to accept the opinion of a number of researchers who consider that in addition to similarities based on genetic consanguinity, a great role is also played in the process of evolution by parallelisms and convergencies (Berg, 1922; Beklemishev, 1952 and others) the elucidation of which will give us the possibility of a more accurate analysis of historical interrelations.

Inasmuch as for further discussions of the question about the phylogenetic ways of development of monogenetic trematodes it is indispensable to bring in special materials we shall stop with what has been said for the time being and will pass on to the questions about the systematics of contemporary forms in order to return again to the questions on the construction of the phylogenetic schemes of the group after this.

CHAPTER II

A SHORT SURVEY OF THE SYSTEMS OF MONOGENETIC TREMATODES

In his "Classen and Ordnungen des Thier-Reichs" Braun (Braun, 1899-1893) expounds in considerable detail the history of the classification of the monogenetic trematodes starting from Zeder (Zeder, 1800) and ending with the exposition of the first variant of the system of Monticelli (Monticelli, 1888). Braun himself accepts the division of monogenetic trematodes into three "families", Temnocephaleae Haswell, Tristomeae Taschenberg, and Polystomeae Taschenberg. As is known at the present time, the first "family" has no relation to monogenetic trematodes. As regards the two others, Braun divides them into a number of "subfamilies." We place both families and subfamilies of Braun in quotations because the names of his "subfamilies" correspond to the presently accepted designation of families, and thus they also must be interpreted in the system of Braun. He divides the "family" Tristomeae into three groups--Tristomidae Beneden with 8 genera, Monocotylidae Taschenberg with 3 genera, and Udonellidae Beneden and Hesse, with 3 genera. In contemporary views of Udonellidae (Ivanov, 1952) this family comprised only two groups characterized, plainly speaking, by the attaching disc being modified into a sucker. All the remaining monogenetic trematodes are separated by Braun into the "family" of Polystomeae subdivided into Octocotylidae Beneden and Hesse with 9 genera, Polystomidae Beneden with 5 genera, Microcotylidae Taschenberg with 4 genera, and Gyrodactylidae Beneden and Hesse with 6 genera. The separation of *Calceostoma* Beneden, *Gyrodactylus* Nordmann, *Dactylogyrus* Diesing and other monogenetic trematodes into one "subfamily" attracts attention as well as the fact that Octocotylidae are separated from Microcotylidae. This system basically was retained until the beginning of the 20th century when Monticelli (Monticelli, 1903) proposed a new classification which represented a considerable step forward, both by quantity of the factual material which went into the basis of the system as well as by the more precise grouping of this material. Characteristic is the exclusion of the family of Temnocephalidae from this group of monogenetic trematodes as animals with undetermined systematic status which was new but completely correct. The basic common classification accepted by Monticelli is mainly based on the nature of the structure of the attaching apparatus. It is completely reproduced below. The subfamilies which were elevated by him into the rank of families are marked by "n" in parentheses, the new families--by "nn" and new subfamilies by an asterisk. p. 334

(Section Oligocotylea[1] Monticelli) p. 335

1. Family Tristomidae Beneden, 1858 (n)
   Subfamily:
      1. Tristominae [genera *Tristomum*, *Trochopus* (=*Placunella*)]
      2. Acanthocotylinae* (genus *Acanthocotyle*)
      3. Ancyrocetylinae [gen. *Ancyrocetyle*, *Epibdella* (=*Phylomella*), *Nitschia*]
      4. Encotyllabinae (gen. *Encotyllabe*).

2. Family Monocotylidae Taschenberg, 1879.
   Subfamily:
      1. Monocotylinae* (gen. *Monocotyle*)
      2. Pseudocotylinae* [gen. *Pseudocotyle* (=*Microbothrium*)]
      3. Calycotylinae* (gen. *Calycotyle*)
      4. Anisocotylinae* (gen. *Anoplodiscus*, *Merizocotyle*, *Lophocotyle*, *Dionchus*).

3. Family Udonellidae Beneden and Hesse, 1868(n).
   Subfamily:
      1. Udonellidae (gen. *Udonella*, *Echinella*, *Pteronella*)

4. Family Calceostomidae Parona and Perugia, 1890(n)
   Subfamily:
      1. Calceostominae (gen. *Calceostoma*, *Fredericianella*)

5. Family Gyrodactylidae Beneden, 1863(n)
   Subfamily:
      1. Gyrodactylinae (gen. *Gyrodactylus*, *Dactylogyrus*)
      2. Tetraonchinae* [gen. *Tetraonchus* (=*Ancyrocephalus*=*Amphibdella*=*Dactylodiscus*)]
      3. Diplectaninae* (gen. *Diplectanum*)

6. Family Dicotylidae(nn)
   Subfamily:
      1. Dicotylinae* (gen. *Sphyranura*)

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[1] There is a misprint--Oliocotylea in the text of the work.

(Section Polycotylea Monticelli)

7. Family Polystomidae Beneden, 1858
   Subfamily:
   1. Polystominae* (gen. *Polystomum*).

8. Family Octocotylidae Beneden and Hesse, 1863
   Subfamily:
   1. Onchocotylinae [gen. *Squalonchocotyle*, *Onchocotyle* (=*Acanthochocotyle*) *Rajonchocotyle*)]
   2. Octocotylinae [gen. *Octocotyle*, *Dactycotyle* (=*Pterocotyle*)]
   3. Octobothrinae* [gen. *Octobothrium* (=*Glossocotyle* + *Ophicotyle*) *Diplozoon*, *Vallisia*.]
   4. Diclidophorinae [gen. *Diclidophora* (=*Choricotyle*), *Cyclobothrium*, *Heterobothrium*]
   5. Plagiopeltinae* [gen. *Hexacotyle* (=*Plagiopeltis*)]
   6. Diaphorocotylinae* (gen. *Erpocotyle*, *Anthocotyle*)

9. Family Hexacotylidae Monticelli, 1899(nn)
   Subfamily:
   1. Diplobothrinae* (gen. *Diplocothrium*)
   2. Plectanocotylinae* (gen. *Plectanocotyle*, *Phyllocotyle*)

10. Family Platycotylidae(nn)
    Subfamily:
    1. Platycotylinae (gen. *Platycotyle*)

11. Family Pleurocotylidae(nn)
    Subfamily:
    1. *Pleurocotylinae* (gen. *Pleurocotyle*)

12. Family Microcotylidae Taschenberg, 1879(n)
    Subfamily:
    1. Microcotylinae* (gen. *Microcotyle*)
    2. Axininae* (gen. *Axine*, *Pseudaxine*, *Gastrocotyle*)

We shall often return to the system of Monticelli but for the time being let us only note from the point of view of the rules of nomenclature the inadmissibility of the use of the names of the families and subfamilies accepted in the present (Monticelli's, *nobis*) system which do not correspond to the type genera.

In 1912 Odhner, studying the question of the homology of the female sex ducts among trematodes and tapeworms, at the same time, came to the conclusion about the necessity of dividing the entire group of monogenetic trematodes into two suborders or superfamilies ("famile-clad") which correspond, in his opinion, to natural relations within the limits of the group under study. He calls the first of these suborders Monopisthocotylea and characterizes it by the presence of a real vagina and the absence of a *canalis genito-intestinalis* and the second--Polyopisthocotylea by the presence of a *ductus vaginalis* and a *canalis genito-intestinalis* (concerning Odhner's point of view on homology of ducts, see page 71). At the same time dhner indicates that if the family of Dicotylidae is to be transferred from Oligocotylea Monticelli into Polycotylea then these artificial groups (as was also noted by Monticelli) become natural and the first of them corresponds to Monopisthocotylea and the second to Polyopisthocotylea. In the same work Odhner indicates that it is inadmissible to consider only the data on attaching organs as sufficient for systematization. Thus, according to his opinion one should not attribute the genera, *Polystoma* (Polystomidae) and *Sphyranura* (Dicotylidae) which are very close to each other, to different families, which understandably for that time was quite correct. In his opinion the internal organization can and must be used as the first basis for systematics, whereas the external structure (=the attaching armature)--second. p. 33o

In 1922, Johnston and Tiegs (Johnston and Tiegs) in their work on Australian monogenetic trematodes made an attempt at a new classification of part of Monogenoidea and established a new superfamily--Gyrodactyloidea (the separation of the systematic groupings was performed by them within the limits of the superfamily). One must note that in this work in addition to regroupings of what is known, the description of a number of completely new forms is included resulting in the possibility of establishing new families, subfamilies, and genera. The superfamily Gyrodactyloidea of Johnston and Tiegs embraces the 2nd, the 4th, and the 5th families in the system of Monticelli plus a new family Protogyrodactylidae including two new genera first discovered by the authors. The changes within the limits of known families as a whole are not very considerable. Thus, within the family Gyrodactylidae the subfamily Diplectaninae is abolished, in connection with the fact that the genus *Diplectanum* is considered as a synonym of the genus *Ancyrocephalus*, and two new subfamilies are included, of which Lepidotreminae is completely new and Merizocotylinae is transferred from the family Monocotylidae. Further, the family Monocotylidae is subjected to changes, within the limits of which the subfamily Anisocotylinae, the genera of which partially pertain to Gyrodactylidae (subfamily Merizocotylinae--is a part of Anisocotylinae) and partially to Calceostomatidae, is abolished. The remaining subfamilies of Monocotylidae remain without changes. The family Calceostomatidae is supplemented by the new family Dionchinae which consists of the genera attributed by Monticelli to Anisocotylinae. It is interesting that Acanthocotylinae are separated from the family Tristomidae as a supplement to the subfamilies of Gyrodactyloidea. At the same time,the authors include the genus Lophocotyle earlier ascribed to Anisocotylinae into the same subfamily. Finally, a new subfamily Protomicrocotylinae with one new genus,Protomicrocotyle (on the basis of the species described by MacCallum),is established as a supplement to Gyrodactyloidea.

Without stopping on smaller works which only have partial significance we should only note two more works before the exposition of contemporary systems.

Thus, in the large résumé of flatworms Poche (Poche, 1925) p. 337 re-examines the system of monogenetic trematodes and his re-examination is not the result of a new independent study of the material but a purely literary work. Nevertheless,in his work there are a number of positive traits,and the system expounded by him deserves to be noted. This system has the following form:

Order Monogenea Carus

1. Tribe Monopisthocotylea Odhner

1. Subfamily Tristomatides nom. nov.
    1. Family Tristomatidae Gambel
    2. Family Udonellidae Taschenberg.

2. Subfamily Gyrodactylides nom. nov. (Gyrodactyloidea Johnston and Tiegs.)
    3. Family Protogyrodactylidae Johnston and Teigs
    4. Family Gyrodactylidae Cobbold
    5. Family Monocotylidae Taschenberg
    6. Family Calceostomatidae nom. nov.

2. Tribe Polyopisthocotylea Odhner

7. Family Polystomatidae Gamble.
8. Family Sphyranuridae nom. nov. (Dicotylidae Monticelli)
9. Family Octocotylidae Monticelli
10. Family Plectanocotylidae nom. nov. (Hexacotylidae Monticelli)

11. Family Platycotylidae Monticelli
12. Family Grubeidae *nom. nov.* (Pleurocotylidae Monticelli)
13. Family Protomicrocotylidae *f. nov.*

What is new in comparison with the preceding system is only the abolition of the family Microcotylidae which was united with Octocotylidae (it was formally proposed by Odhner in 1912) and the introduction of a number of new names instead of the ones proposed by Monticelli on the basis of a number of partially valid considerations. Two genera from the group of Monopisthocotylinea and one genus from Polypisthocotylea remain outside of this system.

Further,a large regroupment was conducted in 1932 by Fuhrmann who divided Monogenoidea into three suborders. His system has the following form:

Order MONOGENA Beneden

1. Suborder Monopisthodiscinea Fuhrmann

1. Family Protogyrodactylidae Johnston and Tiegs (*Protogyrodactylus* and *Trivitellina*).

2. Family Gyrodactylidae Beneden and Hesse
    Subfamily Gyrodactylinae (*Gyrodactylus*, *Dactylogyrus*).
    Subfamily Isancistrinae (*Isancistrum*)
    Subfamily Tetraonchinae (*Tetraonchus* and sp.)
    Subfamily Lepidotreminae (*Lepidotrema* and sp.)

3. Family Calceostomidae (Parona and Perugia) (*Calceostoma*, *Fridericianella* and *Cathariotrema*)

2. Suborder Monopisthocotylinea Odhner

1. Family Monocotylidae Taschenberg
    Suborder Pseudocotylinae (*Pseudocotyle* and sp.)
    Suborder Pseudocotylinae (*Monocotyle* and sp.)

2. Family Tristomidae Taschenberg
    Subfamily Ancyrocotylinae (*Ancyrocotyle* and sp.)
    Subfamily Tristominae (*Tristomum* and sp.)

3. Family Udonellidae Beneden and Hesse (*Udonella*, *Calinella*, *Echinella* and *Pteronella*)

3. Subroder Polyopisthocotylinea Odhner p. 338

1. Family Polystomidae (*Polystoma*, *Sphyranura* and sp.)
2. Family Onchocotylidae Cerfontaine (*Onchocotyle* and sp.)
3. Family Diclidophoridae Cerfontaine (*Diclidophora* and sp.)
4. Family Microcotylidae Taschenberg (*Microcotyle* and sp.)
5. Family Octocotylidae Beneden and Hesse (*Octocotyle* and sp.)

As is seen in the system of Fuhrmann,the suborder Monopisthodiscinea separated by him embraces a large part of the superfamily Gyrodactyloidea of Johnston and Tiegs including Monocotylidae which are ascribed by him to the second suborder. As regards the remaining groups,actually Fuhrmann does not contribute anything new. The significance of the system of Fuhrmann is minimal because he never worked with monogenetic trematodes himself and his considerations about the system bear a purely speculative character.

Later in 1936-1953 appears the series of Price containing the re-examination of the system of monogenetic trematodes on the basis of an independent study of the material. As we shall attempt to show,in spite of the rather significant step forward in the sense that it reflects natural relations of monogenetic trematodes this system nevertheless has a formal character. This system has the following form:

Order MONOGENEA Carus

Suborder Monopisthocotylea Odhner, 1912

Superfamily Gyrodactyloidea Johnston and Tiegs, 1922
1. Family Gyrodactylidae Cobbold, 1877
   Subfamily Gyrodactylinae Monticelli, 1892
   Subfamily Isancistrinae Fuhrmann, 1928
2. Family Protogyrodactylidae Johnston and Tiegs, 1922
3. Family Dactylogyridae Bychowsky, 1933
   Subfamily Dactylogyrinae Bychowsky, 1933
   Subfamily Tetraonchinae Monticelli, 1903
   Subfamily Diplectaninae Monticelli, 1903
   Subfamily Bothitrematinae Price, 1936

4. Family Calceostomatidae (Parona & Perugia, 1890) Price, 1937

Superfamily Capsaloidea Price, 1936
- 1. Family Monocotylidae Taschenberg, 1879
  - Subfamily Monocotylinae Gamble, 1896
  - Subfamily Calicotylinae Monticelli, 1903
  - Subfamily Merizocotylinae Johnston and Tiegs, 1922
  - Subfamily Loimoinae Price, 1936
  - Subfamily Dionchinae Johnston and Tiegs, 1922
- 2. Family Microbothriidae Price, 1936
  - Subfamily Microbothriinae Price, 1938
  - Subfamily Pseudocotylinae Monticelli, 1903
- 3. Family Acanthocotylidae Price, 1936
  - Subfamily Acanthocotylinae Monticelli, 1903
  - Subfamily Enoplocotylinae Tagliani, 1912
- 4. Family Udonellidae Taschenberg, 1879
- 5. Family Capsalidae Biard, 1853
  - Subfamily Benedeniinae Johnston, 1931
  - Subfamily Nitzschiinae Johnston, 1931
  - Subfamily Trochopinae Price, 1936
  - Subfamily Capsalinae Johnston, 1929

Suborder Polyopisthocotylea Odhner, 1912

Superfamily Polystomatidae Gamble, 1896
- 1. Family Polystomatidae Gamble, 1896
  - Subfamily Polystomatinae Gamble, 1896
  - Subfamily Sphyanurinae Price, 1939
- 2. Family Hexabothriidae Price, 1942 p. 339
  - Subfamily Hexabothriinae Price, 1942
  - Subfamily Rajonchocotylinae Price, 1942
  - Subfamily Diclybothrinae Price, 1936

Superfamily Diclidophoroidea Price, 1936
- 1. Family Diclidophoridae Fuhrmann, 1928
  - Subfamily Diclidophorinae Cerfontaine, 1895
  - Subfamily Cyclocotylinae Price, 1943
- 2. Family Discocotylidae Price, 1936
  - Subfamily Discocotylinae Price, 1936
  - Subfamily Vallisinae Price, 1943
  - Subfamily Anthocotylinae Price, 1936
- 3. Family Microcotylidae Taschenberg, 1879
  - Subfamily Microcotylinae Monticelli, 1892
  - Subfamily Protomicrocotylinae Price, 1936
  - Subfamily Axininae Price, 1945 (added new subfamily?)

4. Family Gastrocotylidae Price, 1943
5. Family Mazocraeidae Price, 1936
6. Family Hexostomatidae Price, 1936

Unfortunately, the series of works of Price breaks off on Discocotylidae and the last four families have not been completely analyzed by him but only indicated in his thesis towards his doctoral dissertation (Price, 1936) and in the small article about *Axine* (Price, 1945).

Without stopping at separate works concerning parts of the system of monogenetic trematodes, although they have in a number of cases important significance, for they will be discussed in appropriate places of the exposition of our system, we shall only indicate here that the last general résumé of the systematics of monogenetic trematodes is the work of Sproston (Sproston, 1946) in which the system of monogenetic trematodes basically corresponds to the one proposed by Price with a few exceptions. Thus, in the superfamily Capsaloidea the following changes are made: Enoplocotylinae are transferred from Acanthocotylidae into Microbothriidae as an independent subfamily of the latter; the name of Trochopinae is replaced by Trochopodinae for considerations of linguistic nature; within the limits of Capsalidae one more subfamily is re-established–Encotyllabinae Monticelli 1892 with the unique genus *Encotyllabe* Diesing, referred by Price to Benedeniinae; Acanthocotylidae are removed from the composition of the superfamily Capsaloidea into a special superfamily. Among the suborder of Polypisthocotylea first of all the separation of a new superfamily Avielloidea with one new family Aviellidae and the monotypic genus *Aviella* (=*Ancyrocotyle* Vlassenko) attracts attention (for the history of this much-abused "group" see page 389). Further, within the limits of the family Hexabothriidae, Sproston eliminates the subfamily Rajonchocotylinae, including the genera which pertain to it in the subfamily Hexobothriinae She apparently includes the new family Chimaericotylidae Brinkmann, 1942 in the superfamily Diclidophoroidea; Plectanocotylidae Monticelli, 1903 with two genera (*Plectanocotyle* Diesing and *Octoplectanocotyle* Yamaguti) attributed by Price to Mazocraeidae is included in the family Discocotylidae; from Microcotylidae the genus *Protomicrocotyle* Johnston and Tiegs is transferred to Vallisinae; as regards Microcotylidae, this family is divided by Sproston into two subfamilies--Microcotylinae and Gastrocotylinae, lowering, by this very fact, the group in rank in comparison with the system of Price and not accepting the separation of Axininae; finally, for considerations of nomenclature the name of Cyclocotylinae is replaced by the name Choricotylinae Sproston, 1946.

Thus, at the present time one can consider the system of Price as commonly accepted with separate changes in details put into it by different authors after the period of the appearance of his series of works. p. 340

In 1937 a system different from the ones which have been just expressed was proposed by us. It was based on the study of the development of monogenetic trematodes.

This system remained unknown outside for a number of circumstances and is not even mentioned in the résumés indicated above. As a result of the fact that it represents a basic sketch of the system which is offered in the present work, we do not consider it necessary to deal with it now; its separate peculiarities will be discussed in appropriate places in the text that follows.

Summarizing the short survey of the systems of the monogenetic trematodes we see that they have changed very little in their basic traits starting from the system of Monticelli until the present time. The changes concern mainly details or are connected in a majority of the cases with the appearance of new materials increasing the number of known forms and correspondingly, groups.

The system which is proposed by us at the present time is expanded in detail in the following chapter, it has the following general form:

- Class--Monogenoidea (van Beneden)Bychowsky, 1937
  - Subclass--Polyonchoinea, Bychowsky, 1937
    - A. Order--Dactylogyridea Bychowsky, 1937
      - 1. Suborder--Dactylogyrinea Bychowsky, 1937
        - a. Family--Dactylogyridae Bychowsky, 1933
          - 1. Subfamily--Dactylogyrinae Bychowsky, 1933
          - 2. Subfamily--Ancyrocephalinae Bychowsky, 1937
          - 3. Subfamily--Linguadactylinae Bychowsky, 1957
        - b. Family--Diplectanidae Bychowsky, 1957
          - 1. Subfamily--Diplectaninae Monticello, 1903
          - 2. Subfamily--Rhamnocercinae Monaco, Wood and Mizelle, 1954
        - c. Family--Protogyrodactylidae Johnston and Tiegs, 1922
        - d. Family--Calceostomatidae (Parona and Perugia, 1890) Price, 1937
      - 2. Suborder--Monopisthocotylinea (Odhner, 1912) Bychowsky 1937
        - a. Family--Monocotylidae Taschenberg, 1879

1. Subfamily--Monocotylinae Gamble, 1896
2. Subfamily--Dasybatotreminae Bychowsky, 1957
3. Subfamily--Calicotylinae Monticelli, 1903
4. Subfamily--Merizocotylinae Johnston and Tiegs, 1922
b. Family--Loimoidae Bychowsky, 1957
c. Family--Dionchidae Bychowsky, 1957
d. Family--Capsalidae Baird, 1853
1. Subfamily--Capsalinae Johnston, 1929
2. Subfamily--Megalocotylinae Bychowsky, 1957
3. Subfamily--Trochopodinae (Price, 1936) Sproston, 1946
4. Subfamily--Entobdellinae Bychowsky, 1957
5. Subfamily--Encotyllabinae Monticelli, 1892
6. Subfamily--Nitzschiinae Johnston, 1931
e. Family--Acanthocotylidae Price, 1936
1. Subfamily--Acanthocotylinae Monticelli, 1903
2. Subfamily--Enoplocotylinae Tagliani, 1912
f. Family Microbothriidae Price, 1936

B. Order--Tetraonchidea Bychowsky, 1957
a. Family--Tetraonchidae Bychowsky, 1937
b. Family--Amphibdellatidae (Carus, 1885) Bychowsky, 1957
c. Family--Tetraonchoididae Bychowsky, 1951
d. Family--Bothitrematidae Bychowsky, 1957

C. Order--Gyrodactylidea Bychowsky, 1937
1. Suborder--Gyrodactylinea Bychowsky, 1937 p. 341
a. Family--Gyrodactylidae (van Beneden et Hesse, 1863) Cobbold, 1864
2. Suborder--Polyopisthocotylinea (Odhner, 1912) Bychowsky 1937
a. Family--Polystomatidae (Carus, 1863) Gamble, 1896
b. Family--Sphyranuridae Poche, 1925

Subclass--Oligonchoinea Bychowsky, 1937
A. Order--Diclybothriidea Bychowsky, 1957
a. Family--Diclybothriidae Bychowsky et Gussew, 1950
b. Family--Hexabothriidae Price, 1942
B. Order--Chimaericolidea (Brinkmann, 1952) Bychowsky, 1957
a. Family--Chimaericolidae Brinkmann, 1942
C. Order--Mazocraeidae Bychowsky, 1957
1. Suborder--Mazocraeinae Bychowsky, 1957

    - a. Family--Mazocraeidae Price, 1936
    - b. Family--Hexostomatidae Price, 1936
2. Suborder--Discocotylinea Bychowsky, 1957
    - a. Family--Discocotylidae Price, 1936
        1. Subfamily--Discocotylinae Price, 1936
        2. Subfamily--Diplozooninae Palombi, 1949
    - b. Family--Anthocotylidae Bychowsky, 1957
    - c. Family--Plectanocotylidae Poche, 1925
    - d. Family--Diclidophoridae Fuhrmann, 1928
    - e. Family--Microcotylidae Taschenberg, 1879
    - f. Family--Protomicrocotylidae Poche, 1925
    - g. Family--Gastrocotylidae Price, 1943

CHAPTER III

SYSTEM OF MONOGENETIC TREMATODES

Below is expressed the system of monogenetic trematodes which was basically proposed by us as early as 1937 but supplemented and changed in connection with subsequent works, ours as well as those of numerous Soviet and foreign scholars. The following order of presentation has been adopted: in the beginning a short description is given of the systematic groupings under consideration, then considerations about peculiarities of its evolution, questions linked with the history of its study (to the extent that has a bearing on its foundation) and other remarks of a general nature are cited. Thus the presentation of the system resembles rather a critical analysis. With this one must take into consideration that the questions concerning phylogeny are considered more completely in the next section and consequently are touched only lightly here. p. 342

The system is carried to subfamily; in a majority of cases we shall be forced to dwell on separate genera and sometimes also on intrageneric relations. This is explained by the fact that in some cases the correlation between the families and the subfamilies amalgamated by them are not clear without the analysis of their smaller taxonomic subdivisions.

The divisions or subdivisions accepted by us: class (for its characteristics and discussions see the work dedicated to the relations between monogenetic trematodes and other groups--Bychowsky, 1937, page 1379) subclass, order, suborder, family, subfamily, genus, species (lower taxonomic units are not taken into consideration here because they have been insufficiently studied). We have completely discarded as being inconvenient the category of superfamily, which is accepted by English and American authors and which practically in a majority of the cases for monogenetic trematodes corresponds to suborder.

Class MONOGENOIDEA (Beneden) Bychowsky, 1937[1]

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[1] If one should follow formally the rules of zoological nomenclature, the indication in parentheses of Beneden as the author of the class is erroneous. Actually, the class was established by us under this name for the first time. However, we consider it obligatory to reproduce the name of the researcher who first established the existence of the group and such is undoubtedly van Beneden (van Beneden, 1858). Price

(Price, 1937b) and after him Sproston (Sproston, 1946) and other workers consider that it is not so and indicate Carus (Carus, 1863) as such. The reasons for which the priority of Beneden is not recognized are again purely formal: as Price indicates, in the work of van Beneden the name is only given in the popular appellation (in the French language) ("vernacular name only") and not with the Latin ending.

"Cercomeromorphae, which have the attaching apparatus on the posterior end of the body in the adult condition. The digestive system exists. The development is direct, without changes of hosts. p. 34 The larvae have an intestinal tract. They are parasites of cold-blooded vertebrates and, as an exception on parasitic crustaceans, cephalopods and water mammals." (Bychowsky, 1937)

Subclass POLYONCHOINEA Bychowsky, 1937

"Monogenoidea having larvae with 12 to 16 edge hooks on the attaching disc and for the most part equipped with 4 eyes. The attaching apparatus of the adult forms consists of the chitinous armature located on the attaching disc; the latter can either be altered into a powerful sucker or two to six special suckers can be formed on it. The buccal opening is located between two groups of 'cephalic' glands and it is sometimes equipped with one terminal sucker" (Bychowsky, 1937).

The diagnosis which was given by us earlier is not comprehensive for the group and although it is useful for practical purposes, it nevertheless, requires a series of supplements. Thus, the indication of the presence of chitinous armature among adult forms is not accurate. It is necessary to take into consideration that this armature consists basically of hook-shaped formations which appear either as a grown or developed armature of the disc of the larva, or partially or fully unchanged armature of the larva, or finally partially as armature which existed in the larva and part of which was formed anew in addition to that. As we have already mentioned, the presence of the chitinous "hooked" attaching apparatus among all forms related to the given group does not indicate that the attachment of the adult forms takes place by means of it; very numerous highest forms of this subclass attach themselves with the help of various suckers in the adult state, and the chitinous armature serves only during the early stages of development. Apparently, however, within the limits of this subclass among all forms, with the exception of Microbothriidae the position of which is not clear (see page 385), the chitinous hooks are preserved during the entire life and they are not subject to reduction or metamorphosis. This is very meaningful for the analysis of the consanguinous links of separate groups.

Speaking of the buccal opening and its relation to the cephalic glands,one must not forget that when we indicate two groups of cephalic glands we mean the glands themselves and not the clusters of their effering ducts, the number of which could be greater but is usually paired. There are, however, a few exceptions when in addition to the paired groups of glands, there is one unpaired, lying terminally and opening by one cluster of ducts at the anterior end of the body.

It is not possible to characterize the sex apparatus for the subclass as a whole--so varied in its structure, especially since viviparous forms also enter into the given subclass,

The representatives of the subclass parasitize fishes related to Elasmobranchii, Holocephali (as an exception), and Teleostomi (basic mass). In addition to that they are widely distributed among the Amphibia, Reptilia and Mammalia (?) and they are also encountered on cephalopods. Thus, if one does not take into consideration the parasitizing of the crustaceans,which clearly is of secondary nature, the subclass is scattered in all groups of hosts from which monogenetic trematodes are known at the present time.

This subclass includes all families which pertain to Monopistocotylea according to the systems of Price and Sproston, and part of which also are related to Polyopisthocotylea, i. e., it principally p. 344
differs from the classification of Odhner because it amalgamates forms which have and do not have a *ductus genito-intestinalis*.

The grouping of the forms relative to this subclass is based first of all on the changes of the attaching apparatus which are connected with the changes in the nature of adaptations towards parasitizing on the body of the host. The basic trends of changes can lead in the following three directions: 1) the preservation and development of the chitinous armature in all stages of development; 2) the preservation of the chitinous armature used during the first stages of development, and its functional replacement later by a disc which changes into a powerful sucker; 3) the preservation of the chitinous armature functioning during the first stages of development with its subsequent replacement by a number of suckers formed anew on the attaching disc (see page 328).

With this, one must remember that during the systematization of the forms which pertain to this group on a phylogenetic basis one must bear in mind that the evolutionarily separate forms and their groups can "arrest themselves" at different stages of adaptation within the limits of the basic trends of development and,in such a fashion convergent similarities are possible in any of the three trends or directions;

similarities based on parallelism which arises during the course of the historical process of adaptogenesis.

Three orders--Dactylogyridea Bychowsky, Tetraonchidea Bychowsky, and Gyrodactylidea Bychowsky enter into the subclass.

1. Order DACTYLOGYRIDEA, Bychowsky, 1937

Monopistocotylea Odhner, 1912, part.

Polyonchoinea, which have larvae with 12 to 14 edge hooks[1] on the attaching disc and are, for the most part, equipped with 4 eyes. The attaching apparatus among adult forms consists of a chitinous armature located on the attaching disc: the latter, in a number of species, changes to a powerful sucker. The copulatory organ is either with a chitinous pipe or unarmed. The cephalic end is equipped with two groups of cephalic glands often forming special glandular pulvillae "pillows" which serve for attachment; sometimes the latter form sucker-shaped pits (or cavities, nobis). In the last case these "suckers" are never linked or connected with the buccal opening" (Bychowsky, 1937).

Just as does the diagnosis of the subclass Polyonchoinea, the present diagnosis demands a number of additions and clarifications. The indication of the presence among the larvae of 12 edge hooks is based on information about Protogyrodactylidae and Calceostomatidae; inasmuch as we doubt the correctness of the data concerning Protogyrodactylidae (see page 360) and we are not sure of the correctness of the attribution of Calceostomatidae to this order (see page 363), it probably would have been more correct to consider that the larvae of this order have only 14 hooks. One must also explain that the development of Microbothriidae has not been studied and they are attributed to this order as a supplement on the basis of the similarity between their anatomical structure and that of the families, which clearly belong here, (see page 385) conditionally. As regards the attaching formations of the anterior end of the body, it is characteristic that they are always paired, although basically the cephalic glands decrease in number and are gradually replaced by muscular sucker-shaped formations. In separate cases a secondary increase in the number of glands, as well p. 345

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[1] In connection with the removal of Tetraonchidae and families close to them from this order, the indication of 16 edge hooks is excluded.

as the complication "of the suckers," is observed. Thus, among many Capsalidae the relative number of the glands sharply increases (Nitzschia and others) and among the very independent forms of *Loimos* the head pair of suckers forms a greater number of them secondarily (see page 20).

Egg laying species. The sex systems of the species pertaining here are very diversified, just as is the structure of the sex armature. Two tendencies of the development of the latter are characteristic; in the direction of the strengthening of the chitinous apparatus and sometimes in its considerable complication and--in the direction of a gradual reduction of the chitinous parts and their replacement by purely muscular formations. Within the limits of the order and a number of its families one can observe the increase in the number of testes starting from the initial single one up to a very large number. One cannot fail to note with this that the number of seminal effering ducts does not correspond to the number of testes and, therefore, it is not quite correct to regard this process as polymerization (Dogiel, 1954a).

The representatives of the order parasitize only fishes, mainly Teleostomi and to a smaller degree Elasmobranchii. Only one species is encountered on Holocephali.

This order includes families pertaining to the suborder Monopisthocotylea according to Odhner, with the exception of the family Gyrodactylidae and in this fashion corresponds to it to a certain degree; however, the principles of classification accepted by us do not in any way equal those established by Odhner because the latter separated the group of Monopisthocotylea by the characters of the absence of the *ductus genito-intestinalus* and the presence of a "true" vagina; whereas, we do not attribute great phylogenetic significance to these characteristics.

Within the limits of the order the main directions of its differentiation on the basis of the structure of the attaching armature and its adaptations to different ways of parasitizing the host are easily noticed. One cannot fail to note that along with the progressive development of certain attaching formations we observe frequent cases of reverse nature, i.e., reduction of the separate parts and organs of attachment within the limits of the order. It is indispensable to keep this circumstance in view all the time because we often see similar morphological pictures as a result of convergence during different trends of evolutionary process. These convergencies should never be confused with the converging similarities which appear as a result of the parallel development of separate branches of the phylogenetic tree. As will be seen from that which follows, convergencies based on parallelism during development have a wide distribution in the group under study.

The order consists of two suborders, Dactylogyrinea Bychowsky, and Monopisthocotylinea (Odhner) Bychowsky.

1. Suborder Dactylogyrinea Bychowsky, 1937

Gyrodactyloidea Johnston and Tiegs, 1922, *part.*

Dactylogyridea, having larvae with 12 to 14 edge hooks. The adult forms with attaching discs consisting of the same number of edge hooks, 1-2 pairs of middle hooks which can be absent secondarily, and of a more or less complex connecting apparatus between the middle hooks. Often, on and above the disc are supplementary chitinous hook-shaped formations which serve as the basic armature for the attachment of the worms to the body of the host. p. 346 The digestive system has two intestinal trunks merging at the end or ending blindly. In rare cases the intestinal trunks form lateral outgrowths.

Parasites of marine and fresh water Teleostei

The suborder includes three families--Dactylogyridae Bychowsky, Diplectanidae Bychowsky, *fam. nov.*, and Protogyrodactylidae Johnston and Tiegs. In addition to that, Calceostomatidae (Parona and Perugia) Price are placed here conditionally.

1. Family Dactylogyridae Bychowsky, 1933

Gyrodactylidae Cobbold, 1877, *part.*; Calceostomatidae (Parona and Perugia, 1890) Price 1937, *part.*

Dactylogyrinea, having relatively small or medium sizes in the adult state.[1] The attaching apparatus consists of the chitinous armature including 14 edge hooks, and 1-2 pairs of middle hooks which can be secondarily absent. The chitinous connecting plates which unite the hooks into a single system and located between the middle hooks. In rare cases the connecting formations are absent. Often there are supplementary chitinous parts which serve for the strengthening of the disc and the attachment of the musculature and which enter into the system of armature, but which do not bear by themselves the function of attachment. The cephalic end is equipped with paired clusters of efferent ducts of the cephalic glands; it is flattened and forms 1 - 3 pairs of short tentacle-shaped growths. In the majority of the cases there are 2 pairs of eyes, more seldom one pair; sometimes the eyes can be secondarily absent. The intestinal branches merge at the end or terminate blindly. The ovary is rounded and, more seldom, flask-shaped; the vaginal duct, if it exists, is single; the vitellaria are strongly developed, they are paired; there is only an oötype containing one egg at a time, with the exception of the genus *Linguadactyla* Brinkmann which has a true uterus. The copulatory organ is chitinous; for the most part its pipe is supported by one or several chitinous parts connected with each other and with the pipe, more seldom the connections are absent. The male sex orifice is on the ventral side of the body, for the most part medially.

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[1] Here and later by small sizes is understood the length of worms up to one millimeter, by medium—up to 2 - 5 millimeters and by large - above 5 millimeters.

Parasites of fresh water and marine Teleostei, predominantly Cypriniformes and Perciformes.

In spite of the fact that almost one-half of the known monogenetic trematodes belong to this family its system has been very poorly studied. One must suppose that this is a result of two circumstances; on the one hand, because of the unusual variety of separate chitinous structures, on the basis of which not only species but also the genera are separated; on the other hand, because of the relatively small sizes of the worms, as a result of which the study of their interior structure is considerably impeded. In the present work we do not consider it our problem to analyze this family more in detail, limiting ourselves only to the establishment of basic tendencies of its development and hence to the subdivision into subfamilies and groups within the limits of the latter.

The family includes three subfamilies: Dactylogyrinae Bychowsky, Ancyrocephalinae Bychowsky and Linguadactylinae Bychowsky *subfam. nov.*

1. Subfamily Dactylogyrinae Bychowsky, 1933 p. 347

(Figs. 3, 5, 32, A-C, 33, A-H, 44, 45, 96, 101, A, 108, 111, 119, 120, 132, 134-150, 261, 311, 312, A, B)

Gyrodactylinae Monticelli, 1892, *part.*

Dactylogyridae, having an attaching apparatus with 14 edge and 2 middle hooks; the latter are sometimes absent. The connecting and supplementary plates usually exist, less often the second is absent; among forms without middle hooks there is no connecting apparatus. The intestinal trunks lack lateral outgrowths, they merge at the posterior end. The testis is single; the vaginal duct, for the most part, is at the side of the body, less often on the ventral side, still less often is absent.

Parasites of freshwater and marine Teleostei. The vast majority of species occurs on Cypriniformes.

Type genus, Dactylogyrus Diesing, 1850.

Five other genera pertain hereto: Dogielius Bychowsky, 1936, Falciunguis Akmerow, 1952, Pseudacolpentron Bychowsky and Gussew, 1955, Acolpenteron Fischthal and Allison, 1940, and Paradactylogyrus Thapar, 1948.

Regarding the first two genera there are no doubts that they are derivatives of Dactylogyrus and are very close to it. Likewise, as we show in our common work with Gussew (Bychowsky and Gussew, 1955), without any doubt the genus Pseudacolpenteron originates either from representatives of the genus Dactylogyrus or from ancestors common with the latter, and in such a fashion one can consider its inclusion into the given subfamily as legitimate. The situation of Acolpenteron is more complex. One can hardly doubt that A. nephriticum Gvosdev descends from some sort of species of Dactylogyrus or from forms close to the present genus; whereas, it is impossible to say anything certain about the two remaining species--A. ureterocoetes Fischthal and Allison and A. catostomi Fischthal and Allison. If one can suppose that the second species descends from some sort of Dactylogyrinae or Ancyrocephalinae with an equal degree of probability, the first, on the other hand more probably originates from some sort of Ancyrocephalinae, because only the representatives of the last subfamily are known on Centrarchidae (hosts of the present species). It is very improbable to expect that A. ureterocoetes stems from some sort of Dactylogyrinae and that it switched from parasitizing Cypriniformes (for instance Catostomidae) to Centrarchidae. As we have already indicated with A. V. Gussew, this species, as all other representatives of Acolpenteron and Pseudacolpenteron are forms which were secondarily simplified in connection with the utilization of the new place of habitat on the same species of host (topological origin of conjugate species-genera, according to the terminology of V. A. Dogiel, 1949). Hence, one must recognize it as more probable that the genus Acolpenteron in its present scope, is artificial and its attribution to Dactylogyrinae can be considered as conditional.

One more question arises, is it correct to include the forms in which middle hooks are absent, the number of which, as we have seen earlier represents a very significant peculiarity into the circle of Dactylogyrinae? In other words, would it not be more correct to isolate these forms into a special subfamily? Generally speaking, we attribute great systematic significance to the absence or presence of middle hooks and also to the number of pairs of the latter, and if their absence among Acolpenteron and Pseudacolpenteron were primary we would not have doubted the correctness of the placement of these genera p. 348 into a special subfamily. But since the absence of middle hooks among both genera is a secondary phenomenon, we do not consider it possible to accept this peculiarity as essential in the present case because the difference between the initial and the ones derived from them do not have the nature of new formations which could be used to characterize a new large systematic group.

As regards the genus Paradactylogyrus, its independence is very doubtful and it is more likely that the only species of this genus must be included in the genus Dactylogyrus.

2. Subfamily Ancyrocephalinae Bychowsky, 1937

(Figs. 10, B, 13, 46, 55, A, 65, 79, 92, 101, B and C, 106, 113, D, 118, 121, 151-180, 266, 267)

Tetraonchinae Monticelli, 1903, part.

Dactylogyridae, having an attaching apparatus with 14 edge, 4 middle hooks and connecting plates numbering 2 - 4 which are sometimes absent. The intestinal trunks are without lateral outgrowths with the exception of Tetrancistrum Goto and Kikuchi which has outgrowths. The intestinal trunks terminate blindly or merge at the posterior end. The testis is single. For the most part, the vaginal tract is on the ventral side, less often on the side of the body, often is absent.

Parasites of fresh water and marine Teleostei. The vast majority of species is on Perciformes.

Type genus, Ancyrocephalus Creplin, 1839.

In addition to the type genus, 25 genera belong here:

Actinocleidus Mueller, 1937; *Anchoradiscus* Mizelle, 1941; *Anchylodiscus* Johnston et Tiegs, 1922; *Ancylodiscoides* Yamaguti, 1937; *Ancyrocephaloides* Yamaguti, 1938; *Bychowskyella* Achmerow, 1952; *Cleidodiscus* Mueller, 1934; *Daitreosoma* Johnston et Tiegs, 1922; *Diplectanotrema* Johnston and Tiegs, 1922; *Empleurosoma* Johnston et Tiegs, 1922; *Haliotrema* Johnston et Tiegs, 1922; *Hamatopeduncularia* Yamaguti, 1953; *Heteronchocleidus* Bychowsky, 1956; *Metahaliotrema* Yamaguti, 1953; *Murraytrema* Price, 1937; *Pseudohaliotrema* Yamaguti 1953; *Pseudohaliotrematoides* Yamaguti, 1953; *Pseudomurraytrema* Bychowsky, 1957; *Parancyrocephaloides* Yamaguti, 1938; *Proancyrocephalus* Bychowsky, 1957; *Rhabdosynochus* Mizelle et Blatz, 1941; *Tetrancystrum* Goto et Kikuchi, 1917; *Urocleidus* Mueller, 1934; ? *Anoplocotyle* Polombi, 1943.

The descriptions of various separate genera are very inadequate, especially since some of them were encountered only once and were poorly studied. First of all, this concerns even such important peculiarities as the number of edge hooks and the structure and presence of the connecting plates of middle hooks. Thus, the number of edge hooks among *Ancylodiscoides* was indicated as different by different authors. Yamaguti (Yamaguti, 1937b) wrote that there are only five hooks, Siwak (Siwak, 1932)--12, Zandt (Zandt, 1924--16, whereas actually there are 14 which is shown by numerous data in our researches and that of our collaborators (we have also examined the type species, see also: Bychowsky and Nagibina, 1957). According to Yamaguti, there are 5 edge hooks in the only species of the genus *Ancyrocephaloides*; whereas our verification of material from the same region of research showed that there are 14 of them, just as among other Ancyrocephalinae. At the same time the indication of the absence of connecting plates of middle hooks in the diagnosis of the genus p. 349
Ancyrocephaloides is incorrect. Actually, there are 4 of them although they are very weakly developed and indisputably reduced as a result of the division of each of the two customary plates into two parts as is observed, for instance, among certain species of *Ancylodiscoides*. According to our verification of the factual material it appeared also that 14 edge hooks also exist among *Empleurosoma* (the authors indicated 2 hooks) and *Tetrancistrum* (according to the author the edge hooks are absent altogether, whereas Price, who discovered these hooks first, could not ascertain their exact number).

The only genus remaining without verification is *Daitreosoma*, it probably also has 14 edge hooks and not 2 as is indicated by the author.

As regards the connecting plates of the middle hooks, the data about them are also not always correct. Thus, we have already indicated the errors concerning this in connection with Ancyrocephaloides. Likewise inexact are the data about Parancyrocephaloides in which, during the careful examination of material, we have established that there exists not only a single connecting plate between the ventral hooks but also near each of the dorsal hooks there is a small plate which appears undoubtedly as a result of the bifurcation of the second connecting plate which existed among the ancestors. Thus, among the representatives of this genus there isn't one but three connecting plates. Further among Empleurosoma one connecting plate between the ventral pair of middle hooks is indicated, whereas near the dorsal (lateral, according to the authors) pair--one supplementary plate near each hook; apparently actually these plates merge along the median line of the body and form a common connecting plate. Thus, the basic mass of genera has two connecting plates; in rare cases one of them (the first judging by the time of embryonic development) bifurcates and more rarely the same thing happens with the second (Ancyrocephaloides). One monotypic genus--Protancyrocephalus, in which the middle hooks are altogether without connecting plates, forms an exception.

The internal anatomy of the representatives of this subfamily has been studied even more poorly than the details of the attaching apparatus, in connection with which one cannot consider all the genera attributed here as fully legitimate and probably part of them will be made synonymous with others during further research and part will require further subdivision into separate smaller but independent genera. We do not have the opportunity at the present time to dwell on this question in detail; however, we shall attempt to substantiate the correctness of what has been said before by two examples. Thus, Price (Price, 1937b) indicated that the genus Haliotrema amalgamates species which are very different from each other. As the research of A. V. Gussew (1955), which has already been mentioned (see page 232), showed later, one species of Haliotrema--H. mogurndae Yamaguti--was clearly attributed to this genus erroneously and it should have been transferred into the genus Ancyrocephalus s. lat. One can surmise that H. xesuri Yamaguti (see page 259) also does not belong to Haliotrema but is a representative of a special genus. Thus, apparently 6 species parasitizing Mullidae belong to Haliotrema and it is possible that there are three more species from other families.[1] However, we must not exclude the possibility that

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[1] H. lutianai Yamaguti from Lutianidae, H. ornatum Yamaguti from Apogonidae, and H. caesionis Yamaguti from Pomadasyidae. None of these three species are known to us because they are described in work (Yamaguti, 1953) which is not in the libraries of Moscow and Leningrad.

Price is right and that this genus should be made synonymous with p. 350
Ancyrocephalus. One of the largest differences between these two genera was considered to be the absence of the eyes among *Haliotrema*, however, this is not correct because among *H. spirophallus* Yamaguti, which is at our disposal, there are 4 eyes. It is true that each of them has a very small number of pigmented granules and in addition to that they are relatively clear. Apparently the "glandular cells" of Johnston and Tiegs among *H. australe* Johnston and Tiegs are also eyes as was also correctly suggested by Price (Price, 1937b). Because of this, this characteristic is discarded and the remaining differences between *Haliotrema* and *Ancyrocephalus* can be reduced to details of the sexual apparatus to which one can hardly attribute generic significance.

Conversely, the species united into the genus *Urocleidus* must obviously belong not to one but to several genera. Thus, of the 39 species known to us, 32 have an analogous structure of the copulatory organ in the shape of an elongated pipe fringed by a thin membrane-shaped plate wound around it (Fig. 266). Often this pipe is equipped with a supporting plate, also more or less a common type of structure. During the examination of these 32 species, first of all our attention is attracted by the fact that they fall into three natural groups to which different significance has been attached at different times. First, the species among which both pairs of middle hooks are of the same size (genus *Urocleidus* *s. str.*), then species with one pair of middle hooks twice as large as the other pair (genus *Haplocleidus* *auct.*), and finally species in which the middle hooks have a flat outgrowth in the shape of a plate rounded at the end above the edge or point, which serves apparently for pinching part of the gill filament between it and, the point (genus *Pterocleidus* *auct.*). Of the 32 species of these groups mentioned, 26 are encountered only on Centrarchidae, 4 on Serranidae, 1--Percidae and 1--Catostomidae. The first 3 families of hosts are closely related to each other; i.e., supplemented by the circumstance that only these three families of the superfamily Percoidae occur in the fresh waters of North America where *Urocleidus* *s. lat.* live. Thus, according to occurrence, only the finding of this species on Catostomidae--which are far removed from Perciformes, is an exception. This species--*H. moorei* Mizelle--was encountered in the number of 4 samples *Catonotus flabellaris* (Raf.) in the state of Tennessee (U.S.A.). The description does not give any reason to doubt its belonging to *Urocleidus* *s. str.* in spite of the fact that the author writes that certain peculiarities in structure make this species closer to the genus *Cleidodiscus* (Mizelle, 1940).

As regards the remaining 7 species pertaining to the genus *Urocleidus*, they have a completely different structure of the copulatory apparatus which never bears any membrane-shaped bordering plate on the pipe. At the same time with this, five of them are encountered on Cyprinodontidae (3 species), Poecoelidae (1 species), Amiuridae (1 species), i.e., on fishes far removed from Perciformes which are parasitized by the typical representatives of *Urocleidus*. The remaining 2 species are encountered on Percidae but also sharply differ from *Urocleidus* *s. lat.* in our understanding. Hence, it is understandable that there is nothing surprising in this if we will remember that many representatives of the genus *Ancyrocephalus* and other Ancyrocephalinae are encountered on Percidae. It is interesting that American authors became completely confused in the understanding of the scope of the genus *Urocleidus*. Thus, the type of the genus *U. aculeatus* Van Cleave and Mueller was taken out of this genus relatively recently and in our opinion quite correctly. At the same time, no synoymic conclusions were made from this (see Mizelle and Regensberg, 1945).

All in all one can state with certainty that in its contemporary p. 351
scope the genus *Urocleidus* is artificial. Even if all the three mentioned groups which pertain to groups which we believe should be considered as natural genera are united into one genus, then the 7 remaining species do not in any way belong to *Urocleidus* (*s. lat.*) and should be referred to several of the existing genera of Ancyrocephalinae (apparently part to *Ancyrocephalus* and part to *Cleidodiscus*).

It is clear from what has been said that one can speak only with great reservations about the natural interrelations of the separate genera of Ancyrocephalinae. Nevertheless,during the analysis separate, quite distinct groups are noted. Thus, undoubtedly the genera *Ancylodiscoides*, *Bychowskyella*, and *Hamatopeduncularia*, the representatives of which are characterized by morphological similarity and which parasitize hosts pertaining only to Siluridae and the closely related Bagridae and Ariidae, are close to each other. In spite of the great peculiarity of its attaching apparatus the genus *Anchoradiscus* (Fig. 267) undoubtedly descends from a common root with *Actinocleidus*; both genera parasitize Centrarchidae and are encountered only in America. We have already spoken about the correlations between *Ancyrocephalus* and *Haliotrema* *s. str.* One must only note that in its contemporary scope the genus *Ancyrocephalus* also demands re-examination because in addition to the typical forms in it are included species which do not actually have any relation with it, as for instance *A. cruciatus* (Wedl) which undoubtedly belongs in the group of species close to the genus *Cleidodiscus*, or *A. atherinae* Price which sharply differs by the character of the edge hooks and which appears to be a representative of a special genus.

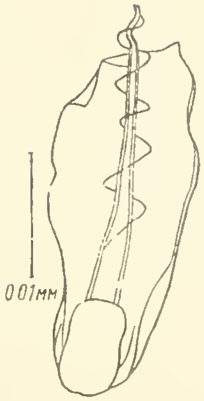

Fig. 266. *Urocleidus* sp., copulatory organ of the worm from the gills of *Pomotis* (=*Lepomis*) *auritus* L. from "Central America."

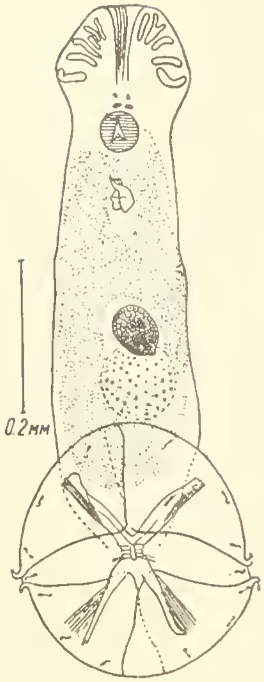

Fig. 267. *Anchoradiscus anchoradiscus* Mizelle, adult worm (according to Mizelle, 1941).

Heteronchocleidus, *Protancyrocephalus*, *Tetrancistrum* and several other "good" genera are separate. As regards *Cleidodiscus*, *Rhabdosynochus*, *Daitreosoma*, and *Empleurosoma*, they demand careful p. 352 re-examination, as was indicated for several genera mentioned above. This work did not enter into the scope of our problem, however, we hope to be able to perform it in the near future.

The inclusion of the genera *Anoplocotyle* and *Anoplodiscus* into Ancyrocephalinae is done conditionally. As regards the first genus, it is possible that it pertains to Calceostomatidae. The presence of an intestine, which has basically the same structure as among *Calceostomella* as well as its occurrence on the caudal fin of the host, i. e., on the surface of the body, as is characteristic for *Calceostoma* and *Calceostomella*, speaks in favor of this. As well as can be judged from the work of Johnston (Johnston, 1930b) the internal organization of *Anoplocotyle* also strongly resembles the last genus. Because of the fact that only one specimen of this monotypic genus was discovered there are no sufficient bases, pending subsequent findings, to be convinced of the correctness of its attribution to this specific family, the veracity of which seems dubious to us, especially since there is an indication of the absence of the chitinous armature of the attaching disc.

The genus Anoplodiscus was described even more poorly than Anoplocotyle (Palombi, 1942b, 1943) and it is possible that it is correctly attributed to Ancyrocephalinae; however, this can be stated with certainty only after subsequent findings.

3. Subfamily Linguadactylinae Bychowsky, subfam. nov.

(Figs. 21, 110, 268-271)

Tetraonchinae Monticelli, 1903, part.

Dactylogyridae having an attaching apparatus with 14 edge, 4 middle hooks and one connecting plate between the first pair of middle hooks. The intestinal trunks have lateral outgrowths terminating blindly at the posterior end. The testis is follicular. The vaginal duct is absent; there is a uterus.

Parasites of marine Gadidae

The type and only genus, Linguadactyla Brinkmann, 1940

The only species known thus far, L. molvae, was described by the author with a great degree of completeness and accuracy. The errors in his work are not numerous. Thus, in describing the attaching armature he points to the presence of 12 (14?) edge hooks: actually there are 14 of them (Fig. 268) as we succeeded in counting on a young sample in our collection. The large middle hooks are described and expressed inaccurately in the work of 1940; in the work of 1952 their figures are more correct. In describing the young worm, Brinkmann indicates the presence in it of one pair of eyes, actually the worms have 2 pairs; however, the front pàir is very small and contain only a few pigmented granules. Adult worms indeed, do not have any eyes and we did not even find traces of them in a number of sections. During the study of the anatomy the author inaccurately depicts "seminal receptacles," representing them as having only one duct entering into the terminal part of the unpaired vitelline duct (Brinkmann, 1940, Figs. 7 and 11). Actually, each of the three "seminal receptacles" has numerous thin ducts which connect it with the cavity of the vitelline duct. There are also other small errors which do not play a principal role, as for instance the inaccurate description of the vitellaria, etc. As p. 353
Brinkmann himself correctly indicated, L. molvae has certain peculiarities of structure which are not encountered in any other known monogenetic trematode at the present time. This pertains to the female sex system; thus, a special correlation between the right and

left half of the vitellaria is characteristic for the species which is now under consideration. They unite by means of a dorsal transversal canal lying somewhat ahead of the anterior end of the ovary; with this the right half of the vitellaria does not have efferent ducts, which in addition to it would have linked it with the rest of the female sex system. This transversal vitelline duct descends on the ventral side exteriorly from the left intestinal trunk and then opens into the oviduct, receiving along the way, from the left half of the vitellaria, the vitelline cells through several ducts which open into it in a rather short area extending from the transverse duct up to the place of its confluence with the "seminal receptacles." The representation of the correlations of the ducts is indicated in Fig. 269 in which we see that they are somewhat different and more complex than Brinkmann draws them (Brinkmann, 1940, Fig. 7). However, it is true that such a thing is not observed among other monogenetic trematodes for whom the presence of differently located efferent ducts of each half of the vitellaria, which then merge and open into the oviduct by a common duct, is characteristic.

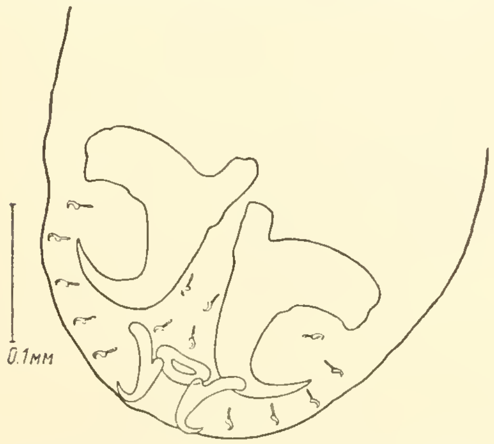

Fig. 268. *Linguadactyla molvae* Brinkmann, attaching disc of the worm from the gills of *Molva dipterygia elongata* (Otto) near the western shores of England (Atlantic Ocean).

The second characteristic peculiar only for *L. molvae* is the presence of 3 "seminal receptacles" and the peculiarities of their structure. As has already been indicated, each of them opens by a cluster of ducts on the anterior surface of the terminal part of the vitelline duct forming 3 rounded sieve-like sections (Fig. 270). First of all, similar sieves are absent in the sex systems of Monogenoidea with the exception that the opening of the vaginas of *Polystoma integerrimum* (and of close species) also open outside by numerous apertures. However, there are no bases to compare these two systems. The function of these "seminal receptacles" is not clear. We cannot consider them as real *receptacula seminis* because in the first place they are relatively very small and in the second place none of the Monogenoidea has them in such number and of such structure. It is clear in the slides that a special tissue which has a peculiar glandular (?) structure lies around each seminal receptacle of *L. molvae*. As an unfounded supposition we can guess that these "seminal receptacles" serve for the resorption of excessive spermatozoids and functionally replace the *ductus genito-intestinalis*. An indication of this is the fact that their location corresponds to the place where the *ductus genito-intestinalis* is located among more highly organized forms.

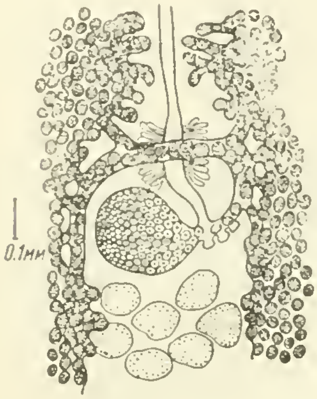

Fig. 269. *Linguadactyla molvae* Brinkmann, middle part of the body, semi-schematically, of the adult worm from the gills of *Molva dipterygia* Sm. from the Norwegian Sea near the Island of Sere.

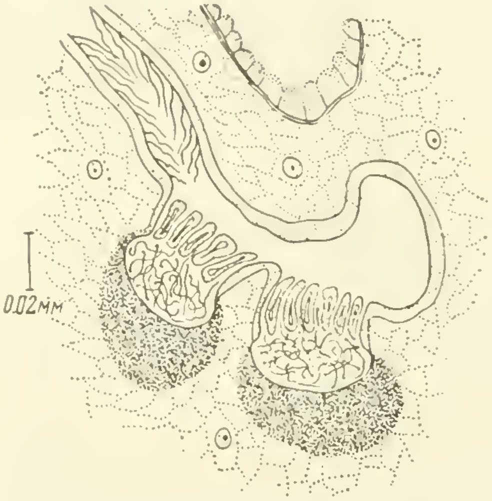

Fig. 270. *Linguadactyla molvae* Brinkmann, cross section through the "seminal receptacles." Worm from the gills of *Molva dipterygia* Sm. from the Norwegian Sea near the Island of Sere.

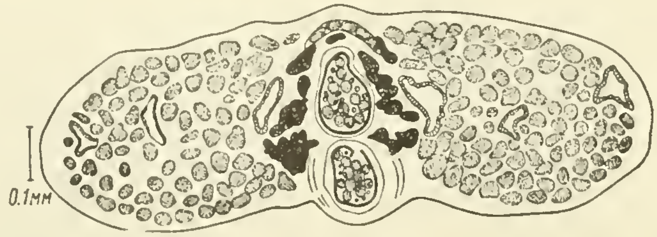

Fig. 271. *Linguadactyla molvae* Brinkmann, cross section in the region of the uterus in the adult worm. The shells of the egg are shown in black. The worm is from the gills of *Molva dipterygia* Sm. from the Norwegian Sea near the Island of Sere.

Finally, as a third characteristic which distinguishes *L. molvae* alone from the rest of the Dactylogyridae is the presence of a real uterus though it is very short and contains only one egg. In such a fashion, mature individuals of *L. molvae* can have two eggs in their p. 354

female sex ducts at the same time in contrast to the remaining Dactylogyridae which can have only one egg. This is clearly apparent from Figure 271.

As regards the structure of the intestinal tract, in spite of the fact that it demonstrates considerable complication in comparison with the rest of the Dactylogyridae, nevertheless the presence of lateral outgrowths near the trunks of the intestine is not characteristic only for the present species. Similar outgrowths are encountered among *Tetrancistrum sigani* Goto and Kikuchi (Ancyrocephalinae) and they are also noticed among *Dactylogyrus iwanowi* Bychowsky (Dactylogyrinae). Apparently the reasons for this phenomenon should be sought in the increase of the general size of the body and not only and even not so much in p. 355
the different phylogenetic state of the separate species. All in all, what has been said before gives adequate reason to consider *L. molvae* as a very specialized species fully deserving isolation into a special subfamily Linguadactylinae.

2. Diplectanidae Bychowsky, *fam. nov.*

Dactylogyridae Bychowsky, 1933 *part.*

Dactylogyrinea having relatively small or middle sizes in the adult state. The attaching apparatus consists of a chitinous armature, which includes 14 edge hooks (indications of the presence of 6 pairs are erroneous) and 2 pairs of middle; the latter are connected by means of 2 (?)--3--5 chitinous plates into a single system. In addition to this, the representatives of this family have special paired attaching formations lying above the disc and also partially on it, on the dorsal and ventral sides in the shape of small rounded convexities equipped with numerous chitinous thorn-shaped little hooks or thin thread-like plates located more or less in concentric rows ("squamodisc"). In a number of cases these convex secondary discs are supplemented by chitinous thorns located across or below the concentric rows of little hooks. Finally, among other species, the secondary discs are replaced by groups of powerful spear-shaped thorns lying in a fixed order on the dorsal and ventral sides of the body and occupying approximately the same location as the secondary discs and apparently are homologous to the chitinous formations of the latter. The anterior end of the body has paired cephalic glands and 2 pairs of eyes. The intestinal branches end blindly and more rarely merge at the posterior end of the body. As a rule the ovary is flask-shaped; the vaginal duct exists, it is single, the vitellaria are strongly developed, paired. The copulatory organ is chitinous, for the most part with only one pipe, more seldom it is complex, with a supporting apparatus.

Parasites of Perciformes, predominantly of marine, less often fresh water Percoidae.

This family is separated by us and combines the representatives of two known subfamilies--Diplectaninae and Ramnocercinae which were ascribed to Dactylogyridae until the present time. Important characters which arise anew in the process of evolution and which bear an obviously progressive nature serve as a basis for the establishment of the new family. Such characteristics, in the first place, are the special attaching formations which appear independently of the usual chitinous armature. These new attaching organs--secondary discs or their derivatives have an important adaptive significance which allows the worms to attach themselves between the gill filaments of the host much more strongly. There is no doubt whatsoever that Diplectanidae originate from Dactylogyridae; however, they are considerably separated from the latter. We can consider that, within the limits of Diplectanidae, the evolutionary development proceeds in the direction of increasingly narrowed adaptability, not only to the host but also to specific sections of the gills of the latter. Thus, the paired species of Diplectanum from Corvina nigra Salv. (D. aculeatum Parona and Perugia, and D. similis Bychowsky) studied by us and also the paired species of Lamellodiscus from Sargus annularis (L.) (L. elegans Bychowsky and L. fraternus Bychowsky) are characterized by their location on different sections of the gills and, even more specifically, p. 356
of the gill filaments and this location is also reflected in the morphological peculiarities of the worms. The attaching apparatus of D. similis and L. fraternus living at the bases of the gill filaments has more elongated connecting plates, in connection with which their attaching disc is also elongated in the lateral direction and its size more or less corresponds to the width of the gill filaments of the host. Hence, the increasingly narrowed adaptability to specific places of habitat (to the microhabitat, nobis) leads to the appearance of supplementary adaptations for the fixation of the animal on the place which is attained by the development of new formations--secondary discs or a system of spear-shaped thorns. It seems to us that it is possible to connect the origin of the secondary discs and the spear-shaped thorns with the cuticular "little scales" possessed by certain Dactylogyridae and which are widely distributed among Diplectanidae (see page 43), the alteration of which apparently gave rise to the specialized chitinous parts of the secondary discs. As regards the spear-shaped thorns, there is no doubt that they are homologous to the armature of the secondary discs. Thus, during the comparison between the structure

of the separate chitinous parts of the system of the secondary discs among different species of Diplectanum we see that they represent separate hook-shaped thorns with more or less well-developed parts and that in a number of cases they acquire rather considerable sizes and the same form as the spear-shaped thorns of Rhamnocercus (Figs. 181 and 272). Examining the question about the primary or secondary nature of the armature of the "discs" and the spear-shaped hooks, we are inclined toward the opinion that the latter are derivations of the former. As a basis for this serves indirect evidence which, however, in our opinion, is sufficiently convincing. Thus, the nature of the location of the spear-shaped hooks is no less strictly determined than that of the separate elements of the secondary discs. Furthermore, among the representatives of Lepidotrema the "discs" are equipped also with thorns of large dimensions and they are apparently very similar to the spear-shaped hooks. Finally, among the representatives of Rhamnocercus, groups of large thorns also appear in the middle part of the disc and, what is most important, along the sides at the places of the location of the middle hooks. This undoubtedly is a secondary phenomenon. Thus, there is all the necessary basis to suppose that Rhamnocercus became separated at a later time than Diplectanum and the genera close to it.

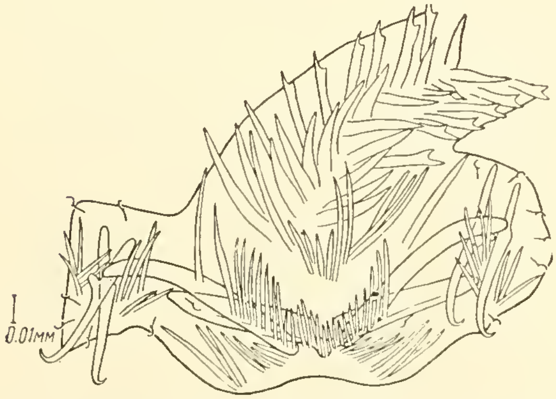

Fig. 272. Rhamnocercus sp., posterior end of the body of the adult animal from the gills of Umbrina nebulosa R. from the region of New York, U.S.A. (Atlantic Ocean).

The combination of Diplectaninae and Rhamnocercinae into a separate family does not arouse the slightest doubt. As Monaco, Wood and Mizelle (Monaco, Wood, and Mizelle, 1954) correctly write, the uniting characters are: 1) the presence of cuticular thorns ("little scales") on the body; 2) dorsal and ventral middle hooks; 3) the similarity of the edge hooks with the ones among Diplectanum, and 4) the presence of connecting plates. Speaking more precisely, there is complete homology between the initial attaching apparatus of Diplectanidae and the one described by Monaco, Wood, and Mizelle, for the species Rhamnocercus rhamnocercus, and of two species which have not yet been published by us. The problem of isolating Rhamnocercus into a separate subfamily is complex. Monaco, Wood, and Mizelle write, that p. 357

as a basis for this serve: 1) the absence of supplementary discs ("squamodisk" of the authors) or cuticular plates in the attaching disc; 2) the presence of separate clusters of needle-shaped hooks which are formed in the parenchyma of the attaching disc and the points of which extend beyond its surface, and; 3) the presence of a number of spear-shaped hooks in the posterior parts of the body ("stem" of the disc). The authors write about this: "The above-mentioned structures just as the thorns in the disc are not cuticular in origin but are from the parenchyma and, in this connection,resemble the middle hooks, the edge hooks and the structures of the copulatory complex."

As we have often indicated earlier, in spite of the fact that the chitinous elements of the disc are incepted in the parenchyma, they are undoubtedly of cuticular origin, and thus the opinion of Monaco, Wood and Mizelle in this connection is erroneous. Erroneous also is their juxtaposition of the armature of the supplementary disc with the spear-shaped thorns lying on the same disc, as well as above it on the "stem" of the body. As has been mentioned before,these are homologous formations. It is obvious that for all the examined structures, even though they be of cuticular origin, their inception can only take place at the expense of the cells lying under the cuticule (cells of the subcuticular epithelium?--compare however, page 41). Taking what has been said into consideration, the first and the third instances which distinguish Rhamnocercinae from Diplectaninae according to Monaco, Wood and Mizelle are interconnected and so to speak both subfamilies differ only by one characteristic--by the change from one type of supplementary armature to another which is homologous to the first. As regards the internal organization, so far we don't know of any morphological differences between the two groups. Nevertheless we are inclined to accept the point of view of Monaco, Wood and Mizelle and to recognize the justification of isolation of the subfamily by taking into consideration the sufficiently sharp break between the structure of the supplementary armature of both groups and particularly taking into consideration the appearance of the thorns on the disc (the second characteristic of the authors) which is, as we have already noted, a secondary phenomenon and new for the group.

The position of the genus Lepidotrema in the system of the family is not clear. Characteristic for it, in addition to the special structure of the secondary attaching armature, is the bifurcation of the lateral parts of the connecting apparatus of the middle hooks--among representatives of this genus there are 5 connecting plates and not 3 as among typical genera of both subfamilies. Apparently this structure is secondary. A basis for this supposition is the fact that among the majority of the lowest Monogenoidea an increase in number of connecting plates takes place, whereas their initial number corresponds to the number of pairs of middle hooks. The presence of 2 plates can be considered as primary for Diplectanidae and only afterwards did the bifurcation of one of them occur, which is analogous to what took place in the genus *Ancylodiscoides* (Fig. 65). Because of this the secondary nature of the appearance of 5 plates instead of 3 by way of the bifurcation of the 2 usual lateral ones is probable.

Thus, if one also takes into consideration that among *Lepidotrema* the structure of the armature of the supplementary discs occupies, so to speak, an intermediary position between *Diplectanum* and *Rhamnocercus*, because it consists of concentric rows of small thorn-shaped p. 358 plates and of large thorns, a question arises whether or not to separate or, to be more precise, to re-establish the subfamily Lepidotrematinae. Unfortunately, at the present time we are not in a position to solve this problem because we do not have a single species of *Lepidotrema* at our disposal and their descriptions in the literature suffer from a number of inaccuracies, particularly in connection with details of the structure of the attaching apparatus.

The family consists of 2 subfamilies--Diplectaninae, Monticelli, and Rhamnocercinae, Monaco, Wood and Mizelle.

1. Subfamily Diplectaninae Monticelli, 1903

(Figs. 14, 34, 56, 59, 70, 113, A, 181-188)

Lepidotremininae Johnston and Tiegs, 1922

Diplectanidae, which have supplementary discs armed with chitinous thorn-shaped little hooks or plates located in concentric rows; sometimes the armature of these discs is supplemented by larger thorns lying across or below the rows of thorn-shaped little hooks. The basic attaching armature is with 2 (?)--3--5 connecting plates.

Parasites of marine and fresh water Percoidae

Type genus, *Diplectanum* Diesing, 1858.

Six more genera also belong here: *Diplectanocotyle* Yamaguti, 1953; *Lepidotrema* Johnston and Tiegs, 1922; *Lamellodiscus* Johnston and Tiegs, 1922; *Pseudolamellodiscus* Yamaguti, 1953; *Squamodiscus* Yamaguti, 1934; and *Neodiplectanum* Mizelle and Blatz, 1941.

As regards the genus *Squamodiscus*, Price (Price, 1937b) supposes that it is synonymous with the genus *Diplectanum*; however, Yamaguti (Yamaguti, 1938) objects to this, in which objection he is supported by Sproston (Sproston, 1946). We think that the opinion of Price is correct but defer final judgment until a more detailed study of the morphology of representatives of both genera is accomplished. As regards the genus Neodiplectanum, its description is very fragmentary and is clearly insufficient. What is interesting here is the fact that the authors described two connecting plates. This undoubtedly would have substantiated our views on the origin of the typical structure of the attaching apparatus of Diplectanidae; however, the drawings in the work of Mizelle and Blatz (Mizelle and Blatz, 1941) are such that we suppose that there is a possibility of error in their assertions. Among the species of Diplectanum which are at our disposal there are some that possess a middle plate of such length that it reaches both pairs of connecting hooks (middle hooks, nobis), and both lateral connecting plates are so tightly pressed against the middle one that on cursory examination it seems that there are only 2 and not 3 plates. Judging from the drawing of Mizelle and Blatz, this error is also not excluded in their case. If this be so, the genus Neodiplectanum has absolutely no right to independent existence. In connection with what has been said in the diagnosis of the family and subfamily, the smaller number of connecting plates is indicated with a question mark.

The genus Lamellodiscus is undoubtedly very close to Diplectanum, its attaching armature appears as if it were the next step in the process of fusion of the separate little parts of the ring of chitinous elements of the supplementary disc.

As regards the genus Lepidotrema, it was already indicated that p. 359
it stands somewhat apart from the rest of Diplectaninae.

The status of the genera Diplectanocotyle and Pseudolamellodiscus is not clear to us (see note on page 349).

2. Subfamily Rhamnocercinae Monaco, Wood and Mizelle, 1954
(Fig. 272)

"Diplectanidae[1]: the attaching disc is equipped with large thorns divided into separate groups, but not forming supplementary discs; there are two pairs of middle hooks (dorsal and ventral) attached by their bases to the middle plates; the edge hooks exist. The "stem" of the attaching disc is equipped with rows of thorn-shaped hooks. Eyes are present. The testes and the ovary are entire, the ovary lies in front of the testes," Monaco, Wood and Mizelle, 1954.

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[1] The authors here give "Dactylogyridae" instead of "Diplectanidae."

Parasites of marine Perciformes; so far known only from Sciaenidae.

The type and only genus, Rhamnocercus Monaco, Wood and Mizelle, 1954.

At the present time the description of only one species, R. rhamnocercus Monaco, Wood, and Mizelle, 1954, from Umbrina roncador Jord. and Gilb. from California (U.S.A.), has been published. Besides this, two more, also from several species of Sciaenidae from North America, which so far have not been described are at our disposal.

The anatomical structure of all species is very similar and is also close to Diplectaninae and basically they differ by the nature of and location and form of the attaching armature and also by the structure of the copulatory organ. The intestinal trunks extend to the beginning of the "stem" and possibly merge at the posterior end.[2] Just as among Diplectaninae the upper part of the ovary embraces one trunk of the intestine in connection with which it has a peculiar retort-shaped form. There is a vaginal duct opening on the side of the body. Just as the authors had supposed the edge hooks number 14 (in their text 12 or 14 are indicated). At the same time, the presence of a cuticular "scale" and the presence of cuticular thorns which is customary for Diplectaninae is characteristic. The latter apparently fall off rather easily among dying specimens, which is described by the authors. This forces us to evaluate the data about the nature of the distribution of the number of chitinous thorns on the "stem" of the disc very carefully. Without any doubt the subfamily is linked genetically more closely with representatives of the genus Lepidotrema than any other.

3. Family Protogyrodactylidae Johnston and Tiegs, 1922

(Figs. 29, 99)

Primitive small worms (Gyrodactyloidea of authors) with greater width than length, with a strongly developed attaching disc bearing 2 pairs of relatively large attaching hooks and numerous small little hooks which are somewhat larger than the usual ones (apparently existing among p. 360 other lowest groups, B. B.). The cephalic glands open in front of the well-demarcated cephalic organs (by clusters of ducts--B. B.). Here also is located the convex (rounded) pharynx. The intestine is divided, its trunks terminate blindly or unite posteriorly. Intestinal outgrowths are absent. Neither the testes nor the ovary are branched. The vagina is absent. The uterus is very short. The cirrus is in the shape of a simple chitinous pipe enclosed in a sac. The vitelline system is very remarkable because it consists of numerous thin "vitelline pipes" located in two groups, one anterior and the other posterior in relation to the ovary. After merging, the transverse vitelline ducts form a longitudinal medial canal or duct which opens into the oötype. The posterior transverse vitelline duct has an obvious junction with the intestinal trunks," (Johnston and Tiegs, 1922).

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[2] This is not clear because of the poor preservation of the material; however, in whole mounts it is apparent that the intestinal trunks approach each other and it is probable that they merge.

To the present family belong 2 genera, Protogyrodactylus Johnston and Tiegs, 1922, (type genus) and Trivitellina Johnston and Tiegs, 1922. Both genera contain one species each and were discovered only by the authors who described them from the gills of Therapon spp. (Serranidae) from the fresh waters of northeast Australia.

In spite of what appear at first sight to be rather detailed descriptions of the representatives of both genera, they are actually very poorly studied. Much of their structure arouses doubt and demands substantiation and redescription. We shall deal with several basic instances. The structure of the attaching armature is not clear. According to the author, the number of edge hooks is 12 among both genera and species; however, the reliability of this seems doubtful to us just as their distribution pictured in the works of Johnston and Tiegs(Johnston and Tiegs, 1922, Table IX, 1 and Table X, 6 and 7) which indicate that the hooks are located in the same places as among the majority of the lowest monogenetic trematodes and that only the 6th pair is absent; it is known that this pair often is of small size and it is possible to think that it was simply not noticed by the authors,especially since errors are known in their work.

The structure of the middle hooks and of their connecting apparatus is also not altogether clear. Based on the very slipshod descriptions and figures of the authors,one can suppose that each of the larger pair of the middle hooks is provided with a supplementary plate analogous (homologous?) with the one among the hooks of Ancylodiscoides,whereas the small pair has a divided middle plate similar to the one among Ancylodiscoides strelkowi Akmerow. If this is so, then it becomes clear that we deal here with the usual scheme of structure of the middle hooks and of the attaching apparatus of both forms among the lowest monogenetic trematodes, and that this essentially does not differ in any way from the ones among representatives of a number of families and in particular among Dactylogyridae.

As regards the internal anatomy, the structure of the sex system, particularly of the vitellaria and their ducts, is most interesting. However, here also not everything seems reliable to us. The presence of the junction of the posterior transverse vitelline duct with the intestine is improbable in our opinion although it is accepted by everybody and this conception has entered all the textbooks where the present family is mentioned. In the text of Johnston and Tiegs concerning *Protogyrodactylus quadratus* Johnston and Tiegs it is indicated that: "the posterior transverse duct possesses a wide lumen and it is very noteworthy that it joins the cavity of the intestinal trunks by means of a large aperture (Table IX, Figure 3)." Similarly, for *Trivetellina subrotunda* Johnston and Tiegs it is p. 361
said that in it the posterior, dorsal transversal duct has the same junction, whereas the ventral lacks it. The corresponding figure for the second genus is not given. As regards the figure to which the authors refer, it is very poorly done and on the basis of it one can suppose, not the junction of the vitelline duct with the intestine but that the authors were dealing with the merging of the intestinal canals which, according to their description, do not join in the first genus. Doubt of the presence of a "vitello-intestinal" junction of such type is forced upon us by considerations of the functional significance of the junction between the intestinal tract and the female sex system. As we showed earlier, this junction has a function in the mass formation of eggs for the discharge of sex products which are not utilized (see page 85). In the structure described by Johnston and Tiegs, such a junction has no significance for it could serve only for the discharge of yolk and only from part of the vitellaria independently of the process of the formation of eggs. We are convinced that subsequent studies will uphold our point of view.

The structure of the vitelline follicles themselves and the presence of the longitudinal vitelline canal is an important distinction of Protogyrodactylidae from the rest of Monogenoidea. These are the only two characters which differentiate the family from the contiguous ones (see however page 360). Hence, we can agree to the presence of the family only conditionally until subsequent redescription of its representatives which will either substantiate its independence or will force us to include both genera united by it into the family Dactylogyridae. We shall also indicate that on *Therapon* spp. are basically encountered representatives of Ancyrocephalinae with which Protogyrodactylidae also have affinities.

One cannot fail to regret that the name of the family and genus *Protogyrodactylus* does not reflect the true nature of the stiuation because even if all their morphological peculiarities are substantiated this will only demonstrate a very high specialization and not primitiveness.

4. Family Calceostomatidae (Parona and Perugia, 1890) Price, 1937

(Figs. 189, 190, 273)

Calceostomidae Parona and Perugia, 1890

Dactylogyrinae, having middle sizes. The attaching apparatus consists of a sucker-shaped disc and its chitinous armature which consists of 12 edge hooks, 2 middle hooks, which sometimes do not differ from the edge hooks in sizes, and middle plates between the middle hooks, which are sometimes absent. The anterior end of the body has two wide cephalic lobes into which open the ducts of numerous glands which do not concentrate into separate clusters. There are 2 pairs of eyes. The intestine is two-branched merging somewhat above the posterior end of both branches; outgrowths are formed both towards the exterior edge of the body and towards the mesial line, as an exception the outgrowths are absent. The copulatory organ is chitinous with a pipe and a supporting apparatus. The testis is single. The ovary is round or flask-shaped with lobe-shaped outgrowths. The vagina is unarmed or with a chitinous pipe, sometimes it is absent (?).

Parasites of marine Perciformes (Sciaenidae and Sparidae) and p. 362
fresh water Cypriniformes (Catostomidae and Ariidae).

Type genus, Calceostoma Beneden, 1852.

In addition to the type genus, 3 more belong to the family --Calceostomella Palombi, 1943; Anonchohaptor Mueller, 1938; and (?) Friedericianella Brandes, 1894.

In spite of the fact that it was established 60 years ago, this family has been very poorly studied. First of all, the questions concerning the presence of edge hooks among its representatives and, in individual cases, about the middle hooks are not clear even at the present time. Thus, in the reference of Price in the diagnosis of the type genus Calceostoma it is indicated that the disc can be unarmed, it is true that this indication is accompanied by a question mark. In the description of the new genus, Calceostomella, which is separated by him, Palombi points to the absence of middle hooks in the only species C. inermis (Parona and Perugia) but notes the presence of edge hooks without indicating their number. Actually all the Calceostomatidae have both middle and edge hooks and the number of the latter is 12, i.e., less than among all the closest families, without considering or counting Protogyrodactylidae among which the number of hooks, as we mentioned before arouses doubt (see page 360). In the genus Calceostoma the middle hooks are connected by rather complex chitinous plates (Fig. 273), whereas among Calceostomella and Anonchohaptor the connecting plates are absent. In Calceostomella the middle hooks have a somewhat different shape and are larger than the edge hooks, but they have a small supplementary chitinous thread possibly homologous to the part of the connecting apparatus of the hooks of *Calceostoma*. As regards *Anonchohaptor*, judging from the description and the figure of Mueller (Mueller, 1938) its middle hooks do not differ in form (?) and size from the edge ones, in connection with which the author also considers them as edge hooks in spite of the fact that they lie in the center of the disc and not along any of its edges as should have been in a similar case.

The genus *Calceostomella* was described by Palombi (Palombi, 1943b) inaccurately. In addition to what has been said before, he writes that the intestinal trunks in *C. inermis* do not merge. This is not true, actually they merge with each other somewhat above the end of both trunks as is apparent from Fig. 189. However, the separation of representatives of the genus *Calceostomella* seems correct to us because the genus is distinguished by the absence of connecting plates between the middle hooks, by a completely different shape of the ovary, by the presence of the vaginal duct and by other more secondary characteristics. Unfortunately we do not have the material on the genus *Calceostoma* and it was not possible to verify the correctness of the indications pointing to the absence of a vaginal duct among its representatives. However, it is very probable that these are errors of researchers, because until recently it was supposed that *Calceostomella inermus* did not have a vagina, the presence of which was shown only by Palombi in 1943.

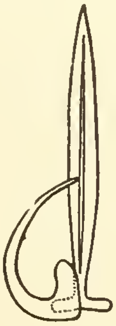

Fig. 273. *Calceostoma calceostoma* (Wagener), middle hook of the disc and its connecting plate. Enlarged 180 times (according to Palombi, 1943).

As regards *Anochohaptor*, in spite of the fact that this genus is sufficiently removed from the two indicated above it nevertheless apparently enters into the circle of the family as Price first indicated (see Mueller, 1938). However, for complete certainty in this case, p. 363
further detailed study of the attaching apparatus and the development of representatives of the present genus is indispensable. The doubts which arise among us are based on the sharp distinction among the hosts and their habitats. In addition to that the structure of the cephalic end in *Calceostoma* and *Calceostomella* apparently differs from that of *Anonchohaptor*. This can only be verified on live or specially fixed material.

The inclusion of the genus *Fridericianella* into Calceostomatidae is made conditionally. This genus, described by Brandes (Brandes, 1894) from the egg of *Arius commersoni* (Lac.) from Brazil has, on the whole, been insufficiently studied.[1] Unfortunately, besides this we did not have the work of Brandes himself and could only use the data from corresponding references. The characteristics which liken this monotypic genus to Calceostomatidae are the shape and peculiarities in the structure of the intestine, and also the presence of relatively very small middle hooks located in the center of the disc. The indication of the absence of edge hooks is apparently erroneous, and their presence and subsequent count will show the correctness of the attribution of this genus to the present family.

The correctness of the inclusion of the present family into Dactylogyridae remains unclear to us because the presence of 12 edge hooks on the attaching disc and a number of other peculiarities point to a considerable singularity of the family from the rest which enter into the circle of the present order. It is quite possible that separation into a special order would have been more correct, but it is impossible to do this at the present time without special morphological study even if it requires going to the basic genera. Consequently, we retain Calceostomatidea conditionally within the limits of Dactylogyridea. It should also be completely clear that their attribution to Dactylogyrinea is not less conditional and is made on the basis of greater similarity between the morphological structures of Calceostomatidae with the ones of the lowest Dactylogyridea.

2. Suborder Monopisthocotylinea (Odhner, 1912) Bychowsky, 1937

Dactylogyridea, having larvae with 14 edge hooks. Adult forms with attaching armature consisting of 14 edge hooks and 1-3 pairs of middle hooks. Connecting plates are absent. In rare cases the attaching armature can be completely absent (Microbothriidae). As a rule the attaching disc is transformed into a more or less powerful sucker which serves for attachment independently of the retention of the chitinous armature among the adult animals. There are cases when the true attaching disc is replaced during development by a false one which develops above on the body of the animal and which assumes the function of attaching the adult animals (Acanthocotylidae). The intestine is in the shape of two trunks merging or terminating blindly, often forming lateral outgrowths and little anastomoses.

Parasites of marine and fresh water Elasmobranchii and Teleostomi.

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[1] The indication of the host demands verification, because undoubtedly the eggs of *Arius* are not the normal place of habitat of the species.

The suborder includes Monocotylidae Taschenberg, Loimoidae Bychowsky fam. nov., Dionchidae Bychowsky fam. nov., Capsalidae Baird Acanthocotylidae Price, and conditionally, Microbothriidae Price.

1. Family Monocotylidae Taschenberg, 1879 p. 364

Monopisthocotylinea, having middle and large sizes in the adult state. The attaching apparatus consists of a sucker-shaped disc divided by muscular septa into separate depressions, and chitinous armature. The latter consists of 14 edge hooks and 2 middle hooks (they are absent among Empruthotrema), and 4 edge hooks are located at the posterior edge of the disc between the middle hooks, whereas the remaining 10 lie along the edge of the disc anteriorly from the middle hooks. The anterior end of the body has two cephalic lobes of different form and often a well-developed adoral sucker. There are 4 eyes among adult forms, they are often subject to scattering which is expressed more or less strongly and more rarely they are completely absent (?). The intestinal tract has two branches not forming outgrowths and terminating blindly. The male sex aperture and the aperture of the uterus are located medially. The copulatory apparatus has a chitinous pipe without a supporting chitinous apparatus. There is one testis rounded or divided into three parts, more rarely there are many testes. The ovary is flask-shaped, embracing one of the intestinal branches. The vaginal ducts are always (?) present. They are single or double.

Parasites of marine Elasmobranchii, and as an exception Holocephali.

Four subfamilies belong here--Monocotylinae Gamble, Dasybatotreminae Bychowsky subfam. nov., Calicotylinae Monticelli and Merizocotylinae Johnston and Tiegs.

The basic leading characteristic of the family is the structure of the attaching disc and not of the attaching armature as among the preceding groups. The reasons for this are quite clear, because the basic role in the attachment of the animals within the present family is played by the disc itself, whereas the attaching armature is used basically during the early stages of development. Apparently the adult animals hardly use either the edge hooks or the middle ones in spite of the fact that in separate species the latter attain rather large sizes.

The basic trends of development of the attaching discs of Monocotylidae are fully determined. One must consider the discs of Monocotyle and Heterocotyle as being the most primitive. They have a distinct octoradial symmetry, thanks to the presence of 8 muscular septa leading from the circular muscular ridge which surrounds the central

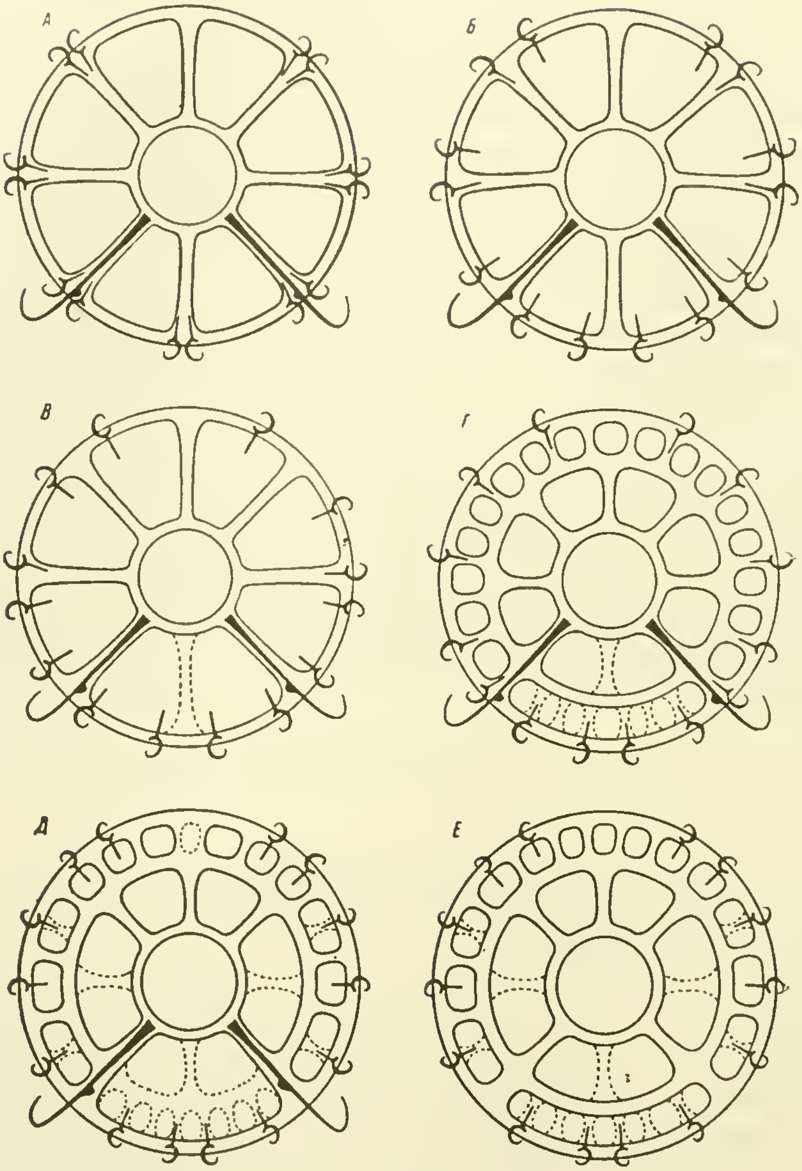

Fig. 274. Diagram of the correlations of the muscular septa and of the chitinous armature of the attaching discs of Monocotylidae. A--Hypothetical form; B--Disc of *Monocotyle* and *Heterocotyle*; C--Disc of *Dasybatotrema* and *Calicotyle*; D--Disc of *Merizocotyle*; E--Disc of *Thaumacotyle*; F--Disc of *Empruthotrema*; the disappearing septa are indicated by a dotted line.

depression and of the same number of cup-shaped depressions lying in between them. However, this octoradial symmetry of the soft parts of the disc is disrupted by the presence of the chitinous armature and the entire system changes to a bilaterally symmetrical one (Fig. 274, B). With this the middle hooks are located in the two posteriormost lateral septa, and in the latest changes in the structure of the disc in this family they retain their location (as will be seen later in the other families of the suborder). In connection with this, the evaluation of the soft and chitinous parts of the attaching apparatus is considerably less burdensome. As regards the edge hooks, apparently they are first located near the margin of the disc directly in the region of the septa, that is in places which have a more firm structure. This is probably connected with the fact that the septa themselves are apparently historically incepted at first in places of the distribution of the musculature and tendons leading from the edge hooks to the center of the attaching disc which can be determined on the basis of the structure of the ones developed in *Calceostomella* and *Dionchus*.

Further changes proceed along the direct line of the reduction in part of the septa on the one hand and, conversely, in the appearance of new secondary septa on the other, with the preservation of bilateral symmetry p. 365
and remnants of the initial octoradial plan of structure. Thus, the discs of *Dasybatotrema* and *Calicotyle*, among which the lowest vertical septum, located between the septa where the middle hooks lie, is reduced are the next evolutionary stage. Along with this, the location of the edge hooks also undergoes a known compensating change which somewhat alters their initial position and they are distributed more equally on the entire circumference of the disc, preserving at the same time the bulk of them toward the posterior part of the disc, which is understandable from the functional point of view because this part undergoes a considerably greater physical load or stress than the upper one during attachment of the animal. With this the edge hooks maintain their position in relation to the middle ones, i.e., four of them remain along the lower edge of the disc between the middle hooks, and the remaining ones lie along the upper edge of the disc (Fig. 274, C). Only part of the hooks remains along the edge of the septa, whereas the remaining ones change into the interseptal space locating along the marginal fringe of the disc.

The appearance of a secondary ring of septa and of the corresponding depressions along the marginal border of the disc constitutes the further change in the structure of the disc. With this, a depression forms in front of each initial septum, i.e., the septum divides, so to speak, and both of its halves separate. At the same time, between these two separated septa one edges in, forming subsequently completely anew, and lies in front of the recession between the two corresponding initial septa. As a result, a system is formed from the central depression of the initial ring of 7 septa with corresponding depressions, and from the secondary ring 18 septa with the same number of depressions. As regards the edge hooks, they lie along the exterior edge at the places where it changes into the secondary septa, little altering their positions in comparison with those of the preceding group (Fig. 274, D). Such a type of structure of the disc is characteristic for Merizocotyle.

Further reduction of the initial ring is characteristic for the following two genera of Monocotylidae--Thaumatocotyle and Empruthotrema, specifically that both middle transversal septa are also subjected to reduction as a result of which there remains only 5 septa and 5 depressions. With this one cannot fail to note, as is clear from the diagrams, (Figs. 274, E and F) that the two upper septa remain unchanged while the reduction of the septa proceeds, so to speak, from the lower edge of the disc. As regards the secondary ring of septa and depressions, their structure is clear from the diagram cited. Apparently one can consider that here took place only the bifurcation of the septum of the original ring (Empruthotrema) with certain complications among Thaumatocotyle. The nature of the distribution of the edge hooks apparently remains the same, but as we did not have our own material we can only say for sure that their correlations with the middle hooks are retained, i. e., 4 hooks lie between the latter and 10 above them. The reduction of the middle hooks among Empruthotrema does not alter these correlations (the 4 lowest edge hooks lie between the two lowest septa).

Finally, the greatest complication is attained by the structure of the disc among Cathariotrema where the formation of a large number of secondary septa and depressions takes place (Fig. 47). Unfortunately, it is impossible to say anything about the nature of these transformations because we did not have the material, and the authors (MacCallum 1916a; Price, 1938a) who studied this form did not attach significance to the accurate representation of the disc and the counting of the number of separate septa or depressions.

The morphological changes of the disc which we have just p. 367
described show that the general direction of the evolutionary process in the given group proceeds along the lines of fragmentation of single sectors of the disc into a larger or smaller number of morphological and functional sections which apparently gives a greater adhesive affect in total than the action of single sucker. One can suppose that this is also true for all the remaining groups which have the attaching apparatus in the shape of a sucker or a system of suckers.

1. Subfamily Monocotylinae Gamble, 1896

(Figs. 27, 48, 72, 80, A, 94, 274, B, 275)

Monocotylidae, having an attaching disc with a central depression and 8 peripheral depressions delimited from each other by muscular septa. The anterior end of the body has 2 lobes into which cephalic glands open and has a weakly developed one adoral sucker. The eyes exist or are absent (?). The vaginal duct is single. The testis is single or divided into three parts.

Parasites of skates, Trigonidae, Rhinobatidae and Myliobatidae,

Type genus, Monocotyle Taschenberg, 1878.

Here belong in addition--Heterocotyle Scott, 1904 and Spinurus Doran, 1953.

The absence of eyes among a part of the representatives of the subfamily indicated above (with a question mark) is apparently erroneous and these data are based on inaccurate observations. All the species which have been studied more carefully appear to have two pairs of small but fully developed eyes. There is no doubt that the genus Heterocotyle is more primitive than the type genus of the subfamily. Thus, their basic differences can be reduced to the presence among the first of the usual rounded testes and among the second of a testis subdivided into three unequal parts. It seems to us erroneous to consider that Monocotyle has three testes as is usually indicated because Goto describes one seminal duct among M. ijime Goto, which shows that the initial presence of a single testis (Goto, 1894) is apparently right. The drawing of Palombi (Palombi, 1942a) in which a separate canal, which fuses somewhat further anteriorly, emerges from each of the front testes arouses doubt, for without resorting to sections, these ducts are very difficult to see and the drawings of Palombi are often excessively schematic and often very inaccurate. Consequently, it is probable that the picture represented by Goto is more likely since the phenomenon of fragmentation of testes without formation of separate seminal ducts is widely distributed among many monogenetic trematodes.

The structure of the attaching disc among the single species of Spinurus, S. lophosoma Doran (Doran, 1953), is of special interest. In p. 368 the disc of the species, which is of the type customary to the subfamily, in addition to the normal armature there are special odd-shaped chitinous thorns located in two rows. The first row, consisting of 8 smaller thorns, lies near the posterior edge of the disc and the second of 6 larger thorns is closer to the central depression of the disc. The edges of all the thorns face the anterior end of the body (Fig. 275). Thus, one observes a considerable similarity between these formations and the thorns of

Rhamnocercinae (see page 356). One cannot doubt that this is a converging similarity, but the formation of analogous peculiarities in different systematic groups is interesting (see page 464).

Let us note also that for *Monocotyle* and *Heterocotyle* the presence of middle hooks of the so-called dactylogyrid-type is characteristic, i.e., --with two extensions of which the exterior is larger than the interior (see Fig. 276, A). Conversely the middle hooks among *Spinurus* are of dasyabototremid-type (see below). This circumstance, a determined form (or common shape, *nobis*) of the hooks is important in the establishment of the relations among Monocotylinae and subsequent subfamilies, as one of the most important characteristics.

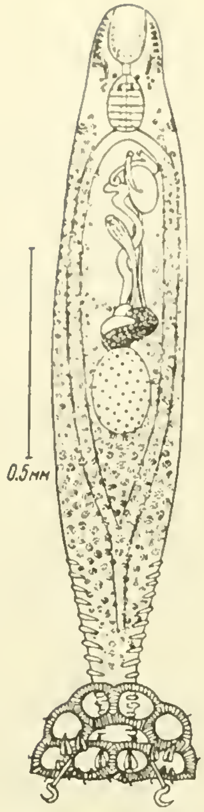

Fig. 275. *Spinuris lophosoma* Doran, adult worm. According to Doran, 1953.

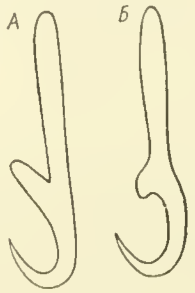

Fig. 276. Hooks of Monocotylidae. A--monocotylidae-type; B--dasybatotremid-type.

2. Subfamily Dasybatotreminae Bychowsky, *subfam. nov.*

(Figs. 32, I, 80, B, 274, C)

Monocotylinae Gamble, 1896, *part.*

Monocotylidae having an attaching disc with a central depression and 7 peripheral ones delimited from each other by muscular septa. The anterior end has a subterminally located, weakly expressed, adoral sucker and a number of cephalic glands opening along the anterior edge. The eyes are absent (?). The vaginal duct is single. The testis is single, it is rounded.

Parasites of skates (Trigonidae).

The type and only genus, *Dasybatotrema* Price, 1936.

Unfortunately we did not possess the material on the single known species, *D. dasybatis* (MacCallum, 1916); however, on the basis of a sufficiently good description of this form in the work of Price (Price, 1938a) we can conclude that this species deserves to be isolated not only into a special genus but also into a special subfamily which occupies an intermediate position between Monocotylinae and all remaining subfamilies. Thus, the basic characteristic which unites *Dasybatotrema* with Monocotylinae is the presence of a single vagina, whereas among the remaining subfamilies it is double. Conversely it will also have in common with the latter the reduction of the posterior middle septa of the attaching disc as well as special structure of the middle hooks. In *Dasybatotrema* these hooks do not have an internal extension but only a small inflation which remains in its place and this inflation corresponds not to the internal extension, but rather to the widening of the basal part of the middle hooks of the dactylogyrid-type (see Fig. 276, C). Such a dasybatotremid-type of hook encountered in the present group is known only in one of the genera of Monocotylinae (*Spinurus*) and is characteristic, with small variations in shape, for Calicotylinae and Merizocotylinae. Taking into consideration what has been said and also that the species examined differs from Calicotylinae by a single p. 369
testis whereas in the latter subfamily there are many of them, and in addition to that, by the considerable differences in the structure of the attaching disc from the one among Merizocotylinae, we consider it quite legitimate to establish the independent subfamily of Dasybatotreminae which stands between Monocotylinae and Calicotylinae in the system.

3. Subfamily Calicotylinae Monticelli, 1903

(Figs. 81, 101, D, 274, C, 277)

Monocotylidae having an attaching disc with a central depression and 7 peripheral ones delineated from each other by muscular septa. As an exception the primary depressions and septa which are located in their usual sites on the disc can disappear and in their places numerous smaller depressions lying in disorder and delimited from each other only by the elevation of the tissue of the disc and not by special septa can be formed (*Dictyocotyle*). The anterior end with a developed adoral sucker and a number of cephalic glands. The eyes exist (always ?), two pairs, among adult animals, acquiring (always ?) the shape of two elongated longitudinal bands. The vaginal ducts are paired. The testes are follicular, numerous.

Parasites of skates (Rajidae and Rhinobatidae), of sharks (Carcharhinidae, Pristiophoridae, Squatinidae, Sphyrnidae) and as a natural exception the chimaera (Chimaeridae).

Type genus, Calicotyle Diesing, 1850

Dictyocotyle Nybelin, 1941 also belongs to this subfamily.

During the study of the representatives of the genus Calicotyle, we succeeded in clarifying two peculiarities in their structure until the present time. Thus, although their edge hooks were suspected, nevertheless, no one had observed them, and consequently no one had attempted to establish their number. During the special study of C. kroyeri Diesing (type species) by us it became clear that this species has 14 edge hooks located as is shown in Fig. 274, C, just as among the remaining Monocotylidae. Thus, one can consider that this question no longer requires further discussion. Furthermore, in spite of the fact that none of the researchers discovered any eyes among Calicotyle, which found reflection even in the diagnoses of the subfamily in the references of Price (Price, 1938a) and Sproston (Sproston, 1946), they actually do have eyes p. 370

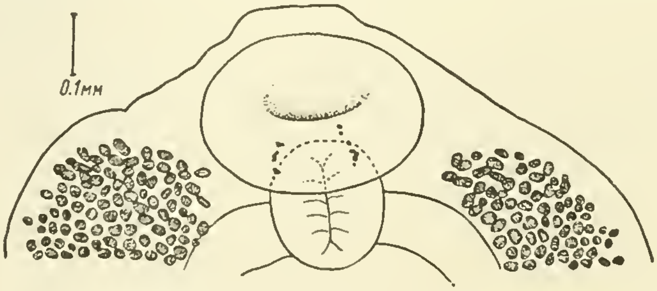

Fig. 277. Calicotyle kroyeri Diesing, anterior end of the body (eyes!) of an adult worm from the skin near the anal opening from Raja batis from the region near western England (Atlantic Ocean).

although of somewhat unusual type (see Fig. 277). The fact that we do not deal with an ordinary occurrence is substantiated by the circumstance that our material on Calicotyle was collected from different regions and from different species of skates. The presence of eyes in the only species of Dictylccotyle--D. coeliaca Nybelin, is not clear. This very aberrant species parasitizes the body cavity of skates, in connection with which the structure of its attaching disc changed secondarily as was indicated in the diagnosis of the subfamily. There is no doubt of its origin from a typical Calicotyle (Nybelin, 1941).

4. Subfamily Merizocotylinae Johnston and Tiegs, 1922

(Figs. 15, 30, 32, L, 47, 101, D, 274, D-F)

Monocotylidae having an attaching disc with a central depression with 7 - 5 depressions adjoining it and a varying number of supplementary ones lying between the edge of the disc and the preceding ones. As an exception the middle hooks of the disc can be absent (Empruthotrema). The anterior end has acephalic glands but lacks a distinct adoral sucker. The eyes exist or are absent (?). Vaginal ducts are paired. The testis is single or divided into two parts.

Parasites of skates (Rajidae, Trigonidae) and sharks (Lamnidae, Carcharhinidae and Sphyrnidae).

Type genus, Merizocotyle Cerfontaine, 1894.

Besides the type genus it also includes Thaumatocotyle Scott, 1904, Empruthotrema Johnston and Tiegs, 1922, and Cathariotrema Johnston and Tiegs, 1922.

The scheme of interrelations between the genera was indicated by us in the remarks on the family. In connection with the indicated tendencies of development of the attaching disc of Monocotylidae and their undoubted evolutionary significance, one cannot agree with the consideration of Brinkmann (Brinkmann, 1940) that the genus Thaumatocotyle is synonymous with Merizocotyle because the nature of the reductions and the new formations of the discs of both genera, even though it seems close, is nevertheless completely different. Unfortunately we did not have our own material of a single one of the genera pertaining to the present subfamily and are consequently deprived of the possibility of verifying a number of data which seems dubious to us. Thus, the absence of eyes among a majority of species demands substantiation, and it is possible that this fact is not correct (sic). Thus, even though Thaumatocotyle is close to the remaining genera, the structure of its disc and its being found in the sharks in contrast to all the others, places it somewhat apart and it is possible that after re-examination it will have to be isolated into a special subfamily. Finally, strange as it may seem at first sight, it seems to us that the absence of middle hooks in Empruthotrema demands further substantiation. It is possible that here takes place the preservation of middle hooks which did not develop in the postembryonic period, i.e., of such sizes that escape the attention of these researchers. Should this be substantiated then the only unexplainable exception among the entire family will be only illusory.

2. Loimoidae Bychowsky fam. nov.

(Fig. 20)

Monocotylidae Taschenberg, 1879, part., Loimoinae Price, 1936.

Monopisthocotylinea, having middle sizes in adult state. The attaching apparatus consists of a sucker-shaped disc, bearing armature consisting of 2 middle, and supposedly, 14 edge hooks; 4 of them along the p. 371 posterior edge between the middle hooks as among Monocotylidae. On the dorsal side of the disc there are two pairs of half-rounded chitinized ribs, sometimes they are weakly noticeable or absent. The anterior end is with 1 - 3 pairs of sucker-shaped depressions located on the dorsal edge of the weakly expressed pre-oral sucker with the opening facing the ventral side. The eyes are absent. The intestine with 2 branches not forming offshoots and ending blindly. The male sex aperture and the opening of the uterus open medially. The copulatory organ with a simple central chitinous pipe. The testis is single, follicular, or there are several of them. The ovaries branch, consisting of a number of separate curved little pipes. The vaginal duct is single.

Parasites of sharks (Sphyrnidae and Carcharhinidae).

Type genus, Loimos MacCallum, 1917.

One more genus, Loimoisina Manter, 1944, enters into the composition of the family in addition to the type genus.

The few representatives of this new family, which is separated by us from Monocotylidae, were poorly described as a whole, consequently much of their morphology remains mysterious. The more detailed data appear in the works of Manter (Manter, 1938 and 1944) which we must use as a basis because of the lack of the material itself. The attaching apparatus of Loimoidae lacks division into separate sections by the septa, which differentiates it from the one of Monocotylidae. However, the location of the middle hooks and their correlations with the edge hooks is of similar nature to that of Monocotylidae. Both families can be completely separated by the presence of the special half-rounded, rib-shaped convex formations on the dorsal side of the disc of Loimoidae, which are apparently of chitinous nature, and which have, as is apparent from the drawing of Manter (Manter, 1944, Fig. 7) a complex structure. Only the sucker-shaped growths of the dorsal side of the disc of Tetraonchoididae (see page 394) are analogous to these formations. What has already been said above forces us to doubt the attribution of Loimos and Loimosina to Monocotylidae; however, besides this these genera also differ by the singular structure of the ovary, which are different not only from Mono-

cotylidae but also from the majority of Monogenoidea. We observe similar structure of the ovary among several forms, as for instance some Calceostomatidae [*Calceostoma calceostoma* (Wagener)] and the highly organized Chimaericolidae, belonging to a completely different group. Price (Price, 1936 and 1938a) isolates *Loimos* into a special subfamily of Monocotylidae--Loimoinae; however, he did not see many peculiarities of these worms. Corrections and additions to his description made by Manter in 1944 show, in spite of the opinion of both authors, that the unification of Loimoinae with the rest of the Monocotylidae is erroneous and this group must be considered as a separate, very specialized family standing somewhat apart in the system of Monopisthocotylinea. We are not at all convinced that its attribution to the suborder indicated is fully justifiable, for even though we write about the probability of the presence of 14 edge hooks, this has not yet been proved. Thus, one must not underevaluate the similarities which exist in the structure of Loimoidae and Calceostomatidae, and in particular the peculiarities of the structure of the sex system, and of the attaching apparatus. As we have already indicated above, the ovary of Loimoidae resembles the one of *Calceostoma calceostoma*, the absence of the connecting plate between the middle hooks is peculiar also for *Calceostomella inermis* (Parona and Perugia) etc. Perhaps only the nature of the location of the middle and edge hooks of the disc, if Manter's above-mentioned drawing is correct, will provide us with greater certainty p. 372
of the correctness of the isolation of Loimoidae to Monopisthocotylinea and not Dactylogyrinea. The occurrence of the family of Elasmobranchii serves as indirect evidence in favor of this also.

3. Family Dionchidae Bychowsky *fam. nov.*

(Fig. 16)

Monocotylidae Taschenberg, 1879, *part.*, Dionchinae Johnston and Tiegs, 1922.

Monopisthocotylinea, having middle sizes in adult state. Attaching apparatus consists of a sucker-shaped disc divided along the periphery by 10 (?)-14, incomplete septa into a number of separate parts, and bearing chitinous armature which consists of 14 edge hooks and 2 middle hooks. All the edge hooks lie along the periphery of the disc and at the places of the termination of the septa and the transition of their musculature into the musculature of the edge of the disc. In connection with this, only one pair of edge hooks lies between the septa in which the middle hooks are located (and one pair of edge hooks) at the posterior edge of the disc. The anterior end of the body is linguaform with 2 relatively long glandular zones into which numerous cephalic glands open. The buccal opening lies on the ventral side and lacks an adoral sucker. There are 4 eyes. The intestine has two branches not forming outgrowths and merging with each other at the posterior end. The male sex opening and the opening of the uterus enter the common genital atrium which opens on the side of the body.[1] The copulatory organ lacks chitinous armature. There are 2 testes lying one behind the other. The ovary is curved or rounded and lies medially from both intestinal branches. The vaginal ducts apparently are absent.

Parasites of Echeneidae and Carangidae.

Type and only genus, Dionchus Goto, 1899.

In the diagnosis the minimal number of septa is indicated with a question mark. This is a result of our doubting the correctness of the data of Goto (Goto, 1899) who describes and pictures the disc of D. agassizi Goto with 10 septa. In our relatively voluminous material from different regions of the World Ocean (probably a spelling error in the Russian and should be Pacific Ocean, nobis), the worms always had 14 septa and, inasmuch as this corresponds to the number of edge hooks, it seems probable to us that Goto committed an error in this case in not noticing the parts of weakly developed septa. All the other data of this excellent researcher are substantiated by our material.

Until this time Dionchus was isolated into a special subfamily as far back as 1922 (Johnston and Tiegs) and was considered as a representative of the family Monocotylidae, which, however, should not be considered correct. Thus, it differs from Monocotylidae (s. str.) by a number of very substantial characteristics. The first of them is the structure of the attaching disc, which appears at first sight similar in both families. However, we have indicated for Monocotylidae the presence of septa which are complete, i. e., they reach the central depression and their number is always such that there is a septum "of the first order" in the middle of the anterior half of the disc, whereas the Dionchidae do not have the middle septum and in its place lies a corresponding depression between the 2 anterior septa (see Fig. 16). At the same time, as is seen from the diagnoses of both families, Dionchus has only 2 and not 4 hooks as in Monocotylidae (s. str.) along the posterior edge of the disc between the septa in which the middle hooks lie. Besides that the number of the septa p. 373
in this section of the disc is different. Among Monocotylidae there is either one septum or there are none, and in Dionchidae this section is equipped with 2 weakly developed septa. Hence, we can conclude that the similarity between the structure of the disc of both families is only of general nature and on the other hand, the differences are quite important.

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[1] A peculiarity which, as is known, is characteristic for tapeworms.

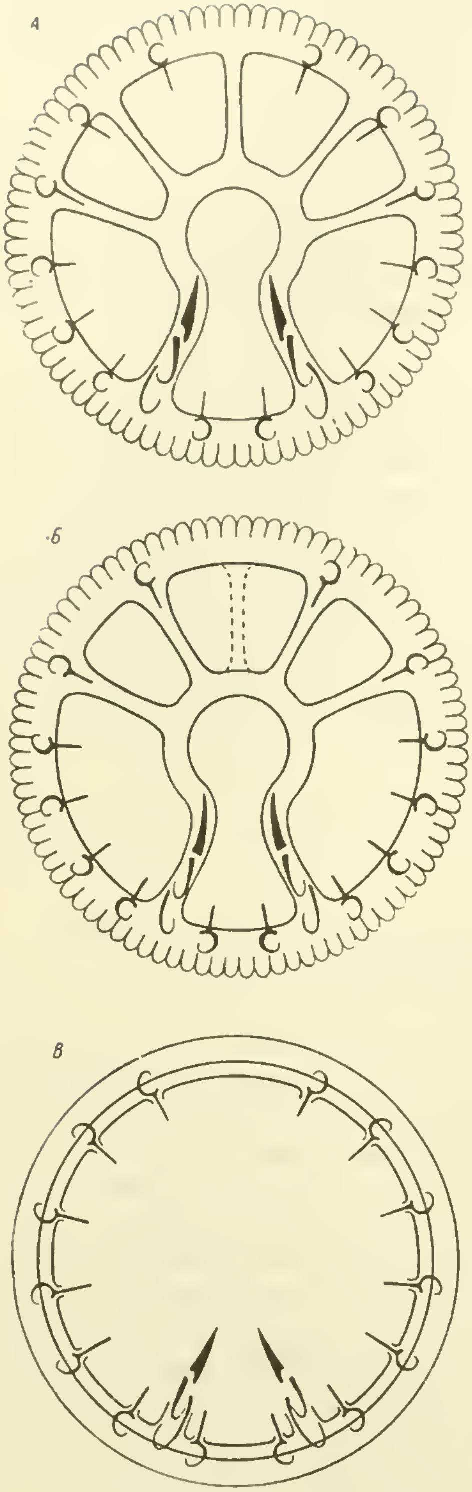
The digestive systems, similar as a whole, differ in the fact that among Dionchidae the trunks of the intestine merge at the posterior end, but not in Monocotylidae. Further, as is obvious from the diagnosis, not less distinct are the differences of the structure of the sex system; they pertain to the peculiarities of the ovary, of the testes, and of the efferent ducts. Particularly substantial are the peculiarities of the location of the ovary--in Dionchidae it is flask-shaped and does not embrace one of the branches of the intestine, which is especially characteristic for Monocotylidae. Thus, one can consider the separation of Dionchidae from Monocotylidae as quite legitimate. As indirect substantiation of this is the parasitizing of bony fishes by the first and of Elasmobranchii by the second.

If we compare Dionchidae with Capsalidae we see a number of important similarities which show that there are close consanguinous ties between these two families which are more important than among both of these families with Monocotylidae. Thus, the presence of one pair of edge hooks in the posterior part of the disc, the common sex aperture at the side of the body, and the absence of armature of the male sex organ are characteristic for all Capsalidae just as for Dionchidae. At the same time the merging of the intestinal trunks at the posterior end of the body is peculiar for a number of Capsalidae. All these characteristics are sufficiently serious to consider that both families are very close to each other.

4. Family Capsalidae Baird, 1853

Tristomidae Cobbold, 1877; Tristomatidae Gamble, 1896; Encotyllabidae Monticelli, 1888.

Monopisthocotylinea, having middle and large sizes in the adult state. The attaching apparatus consists of a sucker-shaped disc divided by muscular septa into a number of peripheral and one central depression and of chitinous armature. In certain cases the septa can be weakly expressed or completely absent. The armature of the disc consists of 14 edge hooks and 2 - 6 middle hooks which can be absent secondarily. In contrast to Monocotylidae and Loimoidae it is characteristic that only 2 edge hooks lie along the edge of the disc between the 2 posteriormost septa in which the middle hooks are located, and the remaining 12 are located in front of the above-mentioned septa. The anterior end of the body has two cephalic adhesive formations having the appearance of glandular fields or more or less well-developed suckers. Between these formations there is a variously expressed head or cephalic lobe. There are 4 eyes. The intestine has numerous external and internal branching outgrowths, as an exception it is simple without any outgrowths. Usually the intestinal trunks terminate blindly, less often they merge with each other. The male sex aperture and the aperture of the uterus open on the side of the



body at the level of the pharynx or somewhat lower; often there is a common sex aperture. As an exception,the sex apertures on the ventral side are almost medial (Nitzschia). The copulatory organ is without chitinous armature. The testes are numerous or there are two. The ovary is rounded or lobe-shaped and lies medially in front of the testes. The vaginal duct is p. 374 single, for the most part it is long and opens on the side of the body from the ventral side (submarginally, nobis) close to the basic aperture; less often it is short and opens on the ventral side of the body between the intestinal trunks.

Parasites of marine, less often transitory (migratory, nobis) Perciformes, Tetrodontiformes, Pleuronectiformes, Acipenseriformes, Mugiliformes, and Selachiformes.

Six subfamilies belong here: Capsalinae Johnston, Megalocotylinae Bychowsky, subfam. nov., Trochopodinae (Price) Sproston, Entobdellinae Bychowsky, subfam. nov., Encotyllabinae Monticelli, and Nitzschiinae Johnston.

The research on Capsalidae was conducted by numerous authors from the end of the 18th century, but

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Fig. 278. Diagram of the correlations of the muscular septa and the chitinous armature of the attaching discs of Capsalidae. A--Capsalinae and Megalocotylinae; B--Entobdellinae and Nitzchiinae; disappearing septum on the diagram B is indicated by a dotted line.

in spite of that there is much that is not clear in the morphology and systematics of this group. Unfortunately, after the excellent work of Goto (Goto, 1894, 1899) the majority of researchers did not attach any significance to a number of the most important characteristics in the description of species, and did not mention them in the texts, accompanying their descriptions by excessively schematic drawings, in which it is impossible to see even such peculiarities as for instance the presence of common or separate apertures of the ducts of the sex system. Hence, it is very difficult to utilize many literary data and, as we shall show later, their authenticity is doubtful.

This concerns, first of all, the structure of the attaching apparatus. The latter in the typical case has the appearance of a powerful sucker divided inside by muscular septa into a number of peripheral depressions and one central depression, and the locations of the middle and edge hooks in relation to the septa are strictly normal for the corresponding group within the limits of Capsalidae. As a rule the majority of authors either do not p. 375
show the edge hooks altogether (Goto, 1894; Meserve, 1938 and others) or show their location on the disc completely arbitrarily (MacCallum, 1921; Price, 1934, and others). Without these data it is very difficult to decide correctly the position of a given species within the system of any subfamily and sometimes even of a genus. Even more sad is the fact that very often one cannot judge even the presence or absence of septa from the data of different authors. In considerable measure the reason for this is that the weakly expressed septa become so transparent during the process of the preparation of slides in Canada balsam that they remain unnoticed.

If we examine the attaching disc of Capsalidae, first of all our attention is drawn by the presence of three basic types of structure. The first type in its most primitive state corresponds to the type of the attaching disc of Calicotylinae, i.e., it consists of 7 peripheral and 1 central depression and the middle hooks (if they exist) lie in the two posterior septa, and on the anterior part of the disc there is one unpaired septum. In contrast to Calicotylinae and Dasybatotreminae the edge hooks are located differently along the edge of the disc, as is apparent from Fig. 278, A. This disc is peculiar for Capsalinae and Megalocotylinae. The second type differs from the first by the absence of the anterior unpaired septum, which never occurs in Monocotylinae and which apparently is a secondary phenomenon in relation to the structure of the disc of the first type. The nature of the location of the chitinous hooks in this type is illustrated in Fig. 278, B. It is encountered in Trochopodinae in the new scope of understanding of this subfamily. Finally the third type, peculiar to Entobdellinae and Nitzschiinae and in the somewhat aberrant species of the subfamily Encotyllabinae, is characterized by the complete absence of septa (see drawing in Fig. 278, C). Further changes of the disc in the different subfamilies will be examined in the corresponding places. Here we shall only note that if the origin of the discs of the second type from the first does not arouse doubt then the question about the primary and secondary absence of the septa in the third type is very complex and apparently comes about differently in different groups.

As regards the internal organization of Capsalidae,its common scheme is very close among all the subfamilies. The basic differences which are of great significance can be reduced to certain peculiarities of structure of the sex and digestive systems. As a matter of fact, it is probable that Monticelli (Monticelli, 1891) was also right when he considered the structure of the head lobe of Capsalidae as important, but this question demands special restudy because no one has studied this family in this connection since his work.

The reconstruction of the system of the family which is presented by us in the present work is very preliminary, and must be defined more exactly,

1. Family Capsalinae Johnston, 1929

(Figs. 1, 4, 35, 57, 58, 76, 95, 101, F, 278, A, 314)

Tristominae Braun, 1893; Tristomatinae Gamble, 1896.

Capsalidae having an attaching disc with a central depression and 7 peripheral ones delimited from each other by powerful muscular septa. p. 376
There is either one pair of middle hooks or they are completely absent. The anterior end has a well-developed cephalic lobe and 2 lateral suckers. The intestinal trunks merge terminally, forming an intestinal ring. The ovary is lobed. The testes are numerous.

Parasites of marine fishes, basically Scombroidei (including Thunnidae).

Type genus, Capsala Bosc, 1811.

Capsaloides Price, 1938, and Tristoma Cuvier, 1817 also belong to the same subfamily.

The systematics of the subfamily were studied by Johnston, (Johnston, 1929) and Price (Price, 1939); however, it demands further substantial revision. Basically, at the present time the structure of the effering ducts of the sex system as well as the existence of dorsolateral chitinous thorns, which exist only in the present group (see page 43), is taken into consideration but little. Both of these systems of indicative signs are without any doubt strictly specific and must be of great systematic significance. The attribution of species to a particular genus is also conditional at the present time. Thus, according to Price (Price, 1939) and Sproston (Sproston, 1946), "Tristomum" foliaceum Goto, 1894 pertains to the genus Capsala although the distribution of the testes in this form does not fit the diagnosis of this genus, etc.

The subfamily is very specialized and lives basically on the skin of fast-moving fishes (an exception--several species from *Mola mola* L.) in connection with which the attaching organs are very powerfully developed. In this connection the middle hooks apparently lose their function very early during the time of postembryonic development and quickly degenerate. Thus, among a number of species, one observes a gradual disappearance of these formations and it is even accompanied by their disintegration. We observe this phenomenon in *Capsala pelamydis* (Taschenberg) from the material from the Black Sea which was transferred to our laboratory by A. V. Rechetnikova. This circumstance is very important because it shows one of the means of disappearance of chitinous attaching organs which are losing their function. It is possible that among aberrant groups of monogenetic trematodes this process proceeded in a similar fashion (see page 347). Unfortunately, the development of Capsalinae was not studied and at the present time we cannot say anything about the initial number of middle hooks on the discs of its representatives. However, there is reason to believe that it equals one pair, i.e., that it sharply differs from other Capsalinae. If this should be proved and, also, if we should take into consideration the peculiarities of the structure of the intestine, of the female sex system, and of certain others, it would be quite probable that this subfamily would have to be transferred to a higher rank, after separating it from the rest of the "tristomid-like" forms.

2. Subfamily Megalocotylinae Bychowsky *subfam. nov.*

(Fig. 278, A, 279)

Trochopodinae (Price, 1936) Sproston, 1946 *part.*

Capsalidae, having the attaching disc with a central, often weakly expressed depression, and an unequal number (mostly 7) of peripheral ones delimited from each other by muscular, sometimes weakly developed septa. The middle hooks number 3 differently developed pairs. The anterior end has a weak or completely undeveloped cephalic lobe, and 2 more or less well-developed suckers, more rarely instead of suckers there are two glandular fields similar to the ones of *Dionchus*. The intestinal trunks have lateral and interior weakly branching outgrowths, they do not merge at the p. 377
posterior end. The ovary is rounded. There are always 2 testes.

Parasites of marine fishes, basically Perciformes, more rarely sharks (Carcharhinidae and Squatinidae).

Type genus, *Megalocotyle* Folda, 1928.

In addition to the type genus, 2 more--*Macrophyllida* Johnston, 1929 and *Sprostonia* Bychowsky *gen. nov.*--pertain to this subfamily.

The present family is removed by us from Trochopodinae, in the old understanding of the latter, on the basis of the structure of the attaching disc which in Megalocotylinae, pertains to the first of the types which were analyzed above and among Trochopodinae (s. str.) to the second. In spite of the fact that both subfamilies are very close in the rest of their characteristics, we consider these differences to be of primary importance.

As regards the genus Megalocotyle, as we have already mentioned earlier (see page 258), M. rhombi (Beneden and Hesse) and M. squatinae (MacCallum), must be excluded from it without any doubt. The last species, attributed to the genus Megalocotyle by Price in 1939, was redescribed by him somewhat earlier (Price, 1937b) from samples collected in Singapore from the gills of Squatina squatina (L.) by MacCallum's son back in 1916. The very inaccurate first description of MacCallum was made on the basis of these collections. The attaching disc of this form has a much more complex structure than among all Megalocotyle while retaining the same basic type of structures. As is apparent from Fig. 279, 2 of the septa are subdivided each into 3, forming 4 more supplementary depressions and in addition to that, in the posterior depression of the disc there are inceptions of 2 incomplete septa, and in both of the anterior ones, one each. Thus, we see here the process of complication analogous to that of Monocotylidae although, it is true, proceeding along more complicated lines. This characteristic can be considered sufficient for separation of this species into a special genus; however, the cephalic end of these worms also has a special structure which also is of important systematic significance. In general traits the anterior end of M. squatinae has the same structure as in Pseudobenedenia, i.e., the anterior edge is equipped with glandular preoral lobes and two more or less strongly developed suckers. All this taken together allows us to consider it necessary to isolate M. squatinae into a special genus--Sprostonia Bychowsky, gen. nov. so far with a single species S. squatinae (MacCallum, 1921) Bychowsky comb. nov.[1]

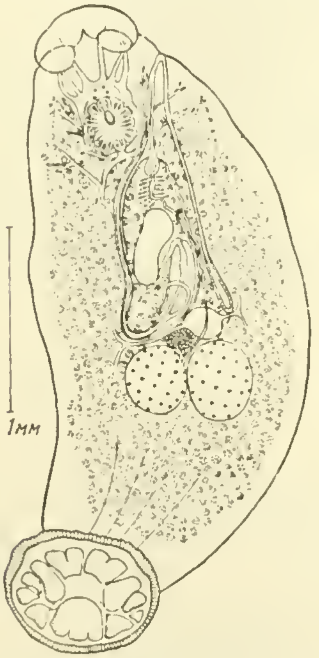

Fig. 279. Sprostonia squatinae (MacCallum) adult worm. (According to Price, 1937).

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[1] The genus is named in honor of N. Sproston, who in her résumé (Sproston, 1946) first pointed to the dubiousness of the attribution of

Its occurrence on sharks can also serve as indirect substantiation of the independence of this genus, whereas all the representatives of *Megalocotyle* (*s. str.*) parasitize Perciformes (see page 258). p. 378

The structure of the disc in *Macrophyllida* is interesting and enables us to clarify the appearance of forms without septa. In this odd worm the two posterior septa, in which the middle hooks are located,[1] do not contain any musculature and are clearly reduced. Johnston writes, in his important work (Johnston, 1930a) that the disc of *M. antarctica* Hughes has 5 peripheral depressions and that its "posterior depression is large and is bisected by two atrophied rays deprived of special musculature." These "rays" represent the disappearing posterior septa of the rest of *Megalocotyle* which is substantiated by the presence of middle hooks in them. Thus, *Macrophyllida* demonstrates one of the possible ways of the disappearance of septa and a very odd one because among a majority of Capsalidae it is precisely these septa which are more powerfully developed and apparently are preserved longer than anything else.

3. Subfamily Trochopodinae (Price, 1936) Sproston 1946

(Figs. 28, 98, 102, 113, C, 196-202, 278, B, 280)

Benedeniinae Johnston, 1931, *part*.

Capsalidae, having the attaching disc with a central, often weakly expressed depression and an even number (6 - 12) of peripheral ones delimited from each other by muscular septa and sometimes weakly developed septa or septa deprived of musculature. The middle hooks number 3 pairs. The anterior end has a weakly developed cephalic lobe and 2 strongly developed suckers. The rest (of the characters are, *nobis*) just as among *Megalocotylinae*.

Parasites of marine fishes, basically Perciformes, but are encountered also on a number of other orders.

S. squatinae to the genus *Megalocotyle*, although she did not make corresponding conclusions from this.

[1] Johnston points to the presence of two pairs of the latter; this is hardly correct; it is more likely than not that he did not notice the third smallest pair as well as all the edge hooks.

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Type genus, *Trochopus* Diesing, 1850.

Into the composition of the subfamily enter also *Benedenia* Diesing, 1858 and *Pseudobenedenia* Johnston, 1931.

The structure of the attaching disc according to the second of the types indicated above is characteristic for the subfamily. At first glance our inclusion of the genera *Benedenia* and *Pseudobenedenia* into its composition appears unwarranted. Earlier both named genera were attributed to the subfamily Benedeniinae Johnston, 1931 which was suppressed by us. Reasons which prompted us to include both genera under discussion into the circle of Trochopodinae lie in the fact that the basic characteristic of Benedeniinae--the absence of septa and of the corresponding depressions of the disc--is inconsequential in connection with these genera. Thus, the genus *Pseudobenedenia* established by Johnston was described rather briefly by him in his work in 1931, but described very much in detail in his little known but solid work in 1937 (the last work was not mentioned by Price or Sproston and is not quoted in their résumés). Even in the first work it is said, concerning the structure of the disc, that it "bears 6 light crests probably homologous to the anterolateral, posterior and posterolateral septa of *Capsala*, the posterior lies between the second and third pairs of hooks, the posterolateral ones curve sideways posteriorly from the anterior pair and the anterolateral septa extend anteriorly and outside from the place of the junction of the disc with the body. These crests are deprived of musculature and do not lead to the development of well-expressed depressions." In the second work these data are repeated and are also substantiated by material based on sections through the disc (Johnston, 1937, Fig. 7). Thus, for *Pseudobenedenia* it is not the absence of septa that is characteristic but their weak expression, which is noted by p. 379 Sproston (Sproston, 1946) in her résumé, although, nevertheless she does not make any conclusions from this.

As regards *Benedenia*, our research on certain species from the Far East shows the presence of more or less well-developed, often quite muscular septa among representatives of this genus. Thus, *B. derzhavini* (Layman) has fully developed muscular septa located just as among *Pseudobenedenia*. The same occurs among *B. sebastodes* (Yamaguti), *B. ovata* (Goto), etc. It is interesting that from the specimen from *Sebastes melanops* Girard which was obtained in 1835 on the Island of Vrangel and which is located in the collections of the Zoological Institute of the Academy of Sciences SSSR we removed from the interior surface of the operculum one specimen of an as yet undetermined species of *Benedenia* with excellently expressed septa and depressions between them. On the body of the fish was seen the imprint of all 7 depressions (one central and six peripheral) in spite of the 120 year period since the moment of fixation! In preparing a slide of the specimen (stained with alumcarmine and mounted in Canada balsam) it appeared that the septa were not noticeable on the latter as a result of the clearing and of the fact that part of the body of the worm was lying under the disc! Only after separation of the disc from the body and preparation of a special slide in glycerin gelatin from it did these septa become fairly apparent. Hence, it is to a certain degree understandable why, in describing separate species, no one has paid any attention to this important peculiarity in their organization. In connection with what has been said we suppose that the presence of septa is characteristic for the entire genus Benedenia and that it should be, just as Pseudobenedenia, transferred to the subfamily Trochopodinae.

As regards the genus Trochopus in its contemporary understanding and scope, it is more probable that it is artificial and that later it will be divided into 2 genera and perhaps even more. Thus, the genus amalgamates species with discs which have from 8 to 12 peripheral septa, while the basic mass of the species has 10 septa and only a few have the larger or smaller number of them. For instance, Tr. goniistii Yamaguti has only 8 septa. At the same time our attention is attracted by the fact that it has a relatively short vaginal duct opening on the ventral side of the body far from the common sex aperture, but not peculiar (similar to that of? nobis) to the typical Trochopus. If one also takes into consideration the data about occurrence (see page 259), one can think with a great degree of probability that this species should be removed from the genus Trochopus (s. str.). However, not having sufficient material in our hands we do not consider it p. 380
possible at the present time to make the corresponding changes, but there is no doubt whatsoever that the question is very timely.

Attention is drawn to the double nature of the structure of the septa of the representatives of the genus Trochopus which were in our hands. Only 2 anterior and 2 posterior septa are provided with a strong musculature, whereas the 6 lateral (3 pairs) have a different nature and resemble more ribs than the typical septa (see Fig. 280). The reasons and significance of such a differentiation are not clear to us but it is very desirable to clarify this during subsequent research.

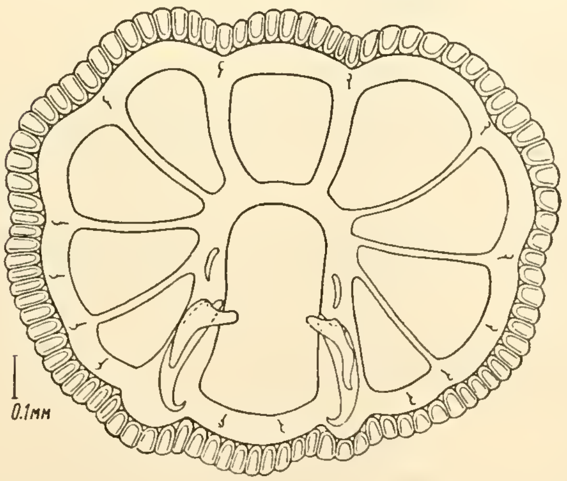

Fig. 280. Trochopus pini (Beneden and Hesse), attaching disc of an adult worm from the gills of Trigla lucerna L. from the Bay of Biscay (Atlantic Ocean).

4. Subfamily Entobdellinae Bychowsky, *subfam. nov.*

(Figs. 278, C, 281, A, 282)

Benedeniinae Johnston, 1931, *part.*

Capsalidae, having an attaching disc deprived of septa and not divided into separate depressions. Middle hooks number 3 pairs. The anterior end with 2 glandular cephalic organs. The rest just as in Megalocotylinae. p. 381

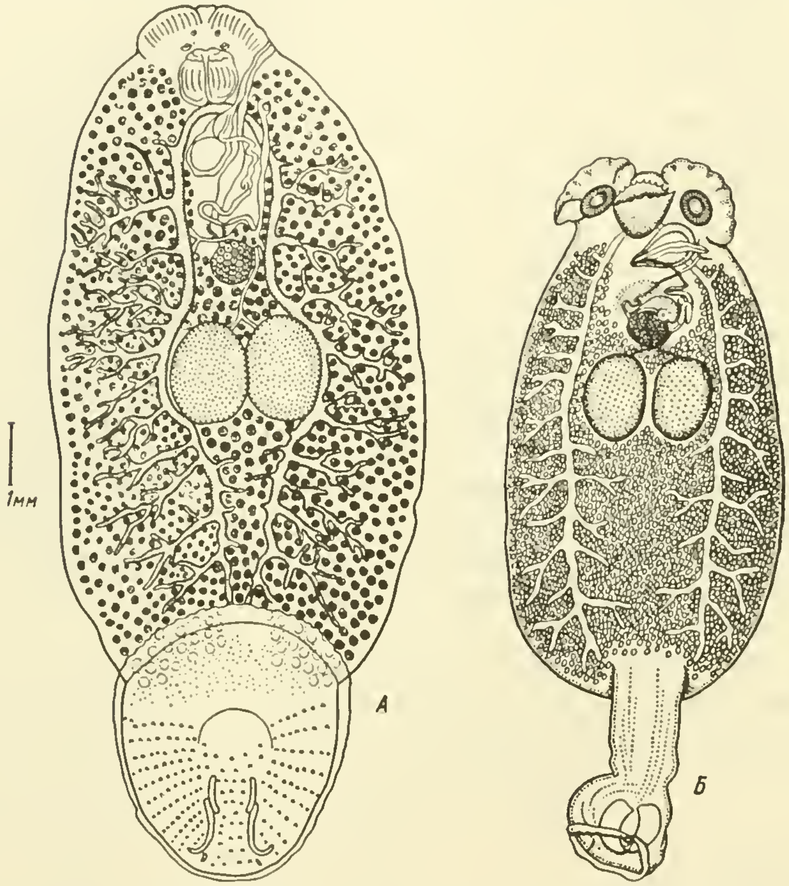

Fig. 281. A--*Entobdella hippoglossi* (Oken), adult worm from the gill cavity of *Hippoglossus hippoglossus* (L.) from the region of the Lofoten Islands (Norwegian Sea); B--*Encotyllabe spari* Yamaguti, adult (According to Yamaguti, 1934). The length is 3.7 mm.

Parasites of marine fishes, basically Pleuronectiformes, more rarely sharks.

The subfamily includes only the type genus, *Entobdella* Blainville, 1818.

The absence of septa on the disc of *Entobdella* either developed very recently or it is a primary phenomenon because there are no traces or remnants of septa that can be discovered on whole mounts or on serial sections of these worms. Besides this the disc of *Entobdella* shows other peculiarities which distinguish this genus from all of the Capsalidae mentioned before. Thus, in the present genus the fringe of the disc, which in Capsalinae, Megalocotylinae and Trochopodinae has a festoon-shaped appearance (see Figs. 1, 28, and 279)[1], is represented as a very waving uninterrupted band, the folds of which sometimes simulate festoons but do not correspond to them (see Fig. 281, A). Further, the fact that among all *Entobdella* the disc is somewhat elongated and has peculiar, rather characteristic outlines which are apparent in the corresponding drawings deserves mention. In such a fashion the "facteur" (general appearance or outline, *nobis*) of the disc, if one may so express it, slightly differs even on superficial examination from the present and other tristomids. Not less important also is the structure of the anterior end which lacks a sucker but has very strong glandular "margins" with a slightly concave ventral (interior) surface. These formations lie on a distinctly delimited section which can be designated as a cephalic lobe. However, this lobe is not identical to the cephalic lobe of the preceding groups, which corresponds only to its middle part and which has a completely different nature (see Fig. 282).

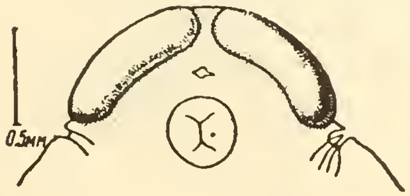

Fig. 282. *Entobdella hippoglossi* (Oken), cephalic "lobe" of an adult worm. On the left on the drawing is seen the opening of the excretory system and on the right the sex aperture. (The left aperture of the excretory system is not visible.)

In connection with everything that has been said above, the unification of *Entobdella*, *Benedenia*, and *Pseudobenedenia* is not justifiable and as a result of this we have to exclude the first genus and place it into an independent subfamily.

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[1] Certain authors sometimes represent it as complete (see for instance: Goto, 1894; Johnston, 1937; Yamaguti, 1940, and others.) This is undoubtedly erroneous.

5. Subfamily Encotyllabinae Monticelli, 1892

(Fig. 281, B)

Benedeniinae auct., part.

Capsalidae having the attaching disc in the shape of a deep, cup-shaped sucker on a more or less long "stem" which is a distinctly narrowed extension of the body. The disc lacks division by septa into parts and is armed with 2 pairs of chitinous middle hooks sharply differing in size and a number of (apparently 14) edge hooks. The anterior end has 2 well-developed suckers equipped with a membranous fringe. The curling of the edges of the middle of the body into the ventral surface is characteristic. The rest is basically as in Megalocotylinae.

Parasites of marine Perciformes and as an exception on coregonids (?)[1]. p. 382

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[1] This indication probably is not correct (see page 262).

Type and only genus, Encotyllabe Diesing, 1850.

Specimens belonging to the present group were not at our disposal, nevertheless, on the basis of studying the literary data we completely agree with Sproston (Sproston, 1946) that the independence of this subfamily should be recognized. The opinion of Price (Price, 1939) about attribution of Encotyllabe to the subfamily of Benedenia cannot be taken into consideration, that is, this genus cannot be linked either to Trochopodinae or to Entobdellinae in the contemporary scope of these subfamilies, and consequently it has to be considered as a representative of a special group.

6. Subfamily Nitzschiinae Johnston, 1931

(Figs. 10, A, 17, 32, H, 61, 68, 109, 193-195, 278, C)

Ancyrocotylinae Monticelli, 1903, part.

Capsalidae, having an attaching disc deprived of septa and divisions into separate depressions. The middle hooks number 3 pairs. The anterior end has 2 strongly developed glandular cephalic organs. The testes are numerous. The remaining--just as among Megalocotylinae.

Parasites of marine and migratory sturgeon-types (Acipenseriformes, nobis).

Type and only genus, Nitzschia Baer, 1827.

In addition to the characteristics enumerated above, a characteristic for the subfamily is the location of all the sex openings on the ventral side behind the pharynx and in front of the ovary in the middle field between the branches of the intestine. The attaching disc is the same as among Entobdellidae (sic), it is deprived of all traces of septa and has a growth border which usually does not even form any noticeable folds.

Addition to the Family

Ancyrocotyle Parona and Monticelli, 1903

(Fig. 283)

This genus, which until the present time was attributed to Benedeniinae, contains only one species--A. vallei (Parona and Perugia, 1895) parasitizing Naucrates ductor (L.) and found only twice--near Trieste (collection of Parona and Perugia) according to the data of Palombi (Palombi 1924c, 1949), and in the regions of the Antilles (material of Price--described under the name of A. bartschi Price, 1934). According to the descriptions of the authors, this species is characterized by the absence of septa on the disc, by 3 pairs of middle hooks, the presence of unbranching intestinal branches which end blindly, by the simple round ovary, 2 testes and weakly developed sex ducts of the usual type (Fig. 283). Attention is drawn to the weak development of the vitellaria of both individuals which were in the hands of Palombi. Apparently he p. 383 possessed immature specimens just as did Price, who stated directly that both of his individuals were immature. Hence, it is more likely that the authors were dealing with stages of development of some Capsalidae and that the independence of this genus demands substantiation. To ascribe this "genus" to Entobdellinae because of the absence of the septa

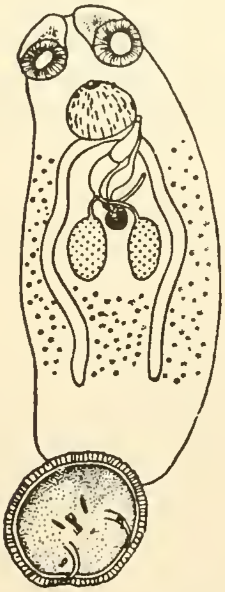

Fig. 283. Ancyrocotyle vallei (Parona and Perugia), general aspect of the worm. Enlarged 30 times. (According to Polombi, 1942).

on the attaching disc would be hardly correct because in the drawing of Palombi (Palombi, 1942b, Fig. 1) the presence of the festoon-shaped fringe, which is not characteristic for the present subfamily but which occurs in Megalocotylinae and Trochopodinae among the groups having 3 pairs of middle hooks, is clearly visible. In connection with what has been said, we do not consider it possible at the present time to attribute Ancyrocotyle to any subfamily of Capsalidae, until receiving completely trustworthy data about the independence of the genus and of a more detailed study of its morphology.

5. Family Acanthocotylidae Price, 1936.

Monopisthocotylinae (sic), having middle or small sizes in the adult state. The attaching apparatus consists of a primary attaching disc armed with 14 edge and 2 middle hooks of the same shape and sizes. Along with this, the adult forms, with the exception of Enoplocotyle, have a large secondary disc lying above the first and armed by a considerable number of special thorns situated in radial rows. As an exception, these thorns can be absent and in their places there are muscular septa. The anterior end of the body with two contractile outgrowths forming sucker-shaped depressions with festoon-shaped edges for the most part. The eyes are absent. The intestines are 2-branched with smooth trunks or forming small outgrowths; as a rule the latter terminate blindly. The male sex aperture lies behind the pharynx between the branches of the intestine. The copulatory organ is unarmed or armed. The testes are numerous or there can only be one. The ovary is round. The opening of the uterus is on the side of the body. There is no vaginal duct.

Parasites of marine Elasmobranchii, Muraenidae and Nototheniidae (?).

The structure of the primary attaching disc, which beyond any doubt corresponds to the disc of the larva emerging from the egg, is characteristic for the family. This is beyond doubt although the development of Acanthocotylidae has not been studied. For all the worms which relate to this family the presence of 16 chitinous attaching hooks, of which 14 are located along the periphery of the primary disc and are undoubtedly homologous to the edge hooks of the remaining monogenetic trematodes, is characteristic. As regards the two hooks lying in the middle of the disc, the question about them is not altogether clear. Morphologically it does not seem possible to differentiate them from the edge hooks and in this connection they can be interpreted either as edge hooks which took up the central position on the disc or as actual middle hooks. In the first case the ancestors of the family must be sought among the lowest forms which have 16 edge hooks, while the second--among those equipped with 14 hooks. It is unlikely that such could be 16-hooked Gyrodactylidae, for the copulatory

organ of Acanthocotylidae and in particular Lophocotyle is clearly of the dactylogyrid-type and not gyrodactylid. Thus, in both cases the ancestors of Acanthocotylidae should be sought only among the same order to which we ascribe this family. However, it is difficult to solve the above-mentioned question without special research. We are inclined to think that the hooks of the disc lying in the middle are truly middle hooks derived p. 384
by analogy from Calceostomatidae, among which the edge and the middle hooks are very similar in structure during the early stages of development. Nevertheless, the point of view of Sproston (Sproston, 1946), who separates Acanthocotylidae into a special superfamily Acanthocotyloidea Sproston, 1946, deserves considerable attention. A basis for this, according to Sproston, is the presence of a secondary disc among adult forms which, as she writes, are absent among all other Monogenoidea. However, Sproston retains only 2 genera--Acanthocotyle and Lophocotyle--within the limits of the family Acanthocotylidae, excluding from it the genus Enoplocotyle which does not retain a secondary disc. This is not correct and does not reflect the true relations of the genera enumerated which have obviously close relationships with each other. This alone indicates that it is hardly permisible to accept the system of Sproston or another analogous system without supplementary research, particularly on the development of all three genera enumerated above. Consequently, we temporarily leave Acanthocotylidae within the limits of Monopisthocotylinea although this may not be altogether correct.

Price (Price, 1936, 1938a) divides Acanthocotylidae into two subfamilies--Acanthocotylinae Monticelli, 1903 and Enoplocotylinae Tagliani, 1912 which seems fully justifiable to us.

1. Subfamily Acanthocotylinae Monticelli, 1903

(Figs. 18, A, 55, B, 112, 113, D, 313)

Acanthocotylidae, having, in addition to the primary, a well-developed secondary disc which is armed or unarmed with thorns. The trunks of the intestine are with or without lateral outgrowths. The testes are numerous.

Parasites of the skin of skates and Nototheniidae (?).

Type genus, Acanthocotyle Monticelli, 1888.

In addition to the type genus another--Lophocotyle Braun, 1896--also belongs to the subfamily.

The powerful development of the secondary attaching disc on which are located a considerable number of peculiar cuticular thorns lying in regular radial rows is characteristic for *Acanthocotyle*. The primary attaching disc lies at the posterior edge of the secondary disc and is characterized by very weak development. An impression is created that either it does not grow at all or almost does not grow after the settling of the larva on the skin of the host just as its edge and middle hooks apparently do not grow.

Apparently the same peculiarities of the primary disc are also characteristic for *Lophocotyle*. As regards this genus, it differs from *Acanthocotyle* by a number of very substantial characteristics, part of which are fully authentic and part of which arouse doubt, just as does the finding of the single species on Nototheniidae as was indicated before (page 275). One must refer the presence of the chitinous pipe of the copulatory organ, which is completely absent among Acanthocotyle, to the authentic differences. This characteristic, i.e., the presence of the pipe, undoubtedly is peculiar to forms more primitive in structure and hence *Lophocotyle* can be considered as closer to the ancestral genera than to *Acanthocotyle*. The location of the opening of the uterus not on the side of the body but on its ventral surface is not less important, and also a more primitive characteristic of *Lophocotyle*. We consider the absence of chitinous thorns on the secondary disc of *Lophocotyle* to be the most important unsubstantiated characteristic. It is doubtful that during the process of evolution their appearance was sudden, it is more likely that p. 385
they developed from cuticular formations analogous and perhaps homologous to the ones among Diplectanidae. In addition to that, the secondary disc of Acanthocotylinae generally resembles the supplementary discs of the representatives of this family very much, both by its place of inception and by the characteristics of its "thorns," We cannot say now whether this similarity appears as a result of a common origin or whether here takes place a coarse convergence, because of insufficient material to make authentic conclusions, but later it will be necessary to give the most meticulous attention to this similarity (see page 466). Returning to the absence of thorns along the disc of *Lophocotyle*, we think it probable that they are absent as a result of improper fixation of both examples known at the present time, which is noticed by the author of the species himself (Braun, 1896) and by Price (Price, 1938a). In any case this question demands re-examination. As regards the nature of the septa of the secondary disc of *Lophocotyle*, they are not described clearly enough to permit the formulation of any basic conclusions on the subject. On the whole, in spite of all the shortcomings of the description there is no doubt that the genus *Lophocotyle* is very close to *Acanthocotyle* and is more primitive.

2. Subfamily Enoplocotylinae Tagliani, 1912

(Fig. 18, B)

Acanthocotylidae, having only the primary disc. The trunks of the intestine are without outgrowths. The testis is single.

Parasites of the skin of Muraenidae.

Type and only genus, Enoplocotyle Tagliani, 1912.

In contrast to the preceding one, the occurrence of growth of the primary attaching disc during the postembryonic period is characteristic for the present subfamily. Apparently all the chitinous hooks also grow, although not noticeably, because we deal here with a single attaching apparatus in all stages of life of these worms. If one is to compare Enoplocotyle with representatives of Acanthocotylinae there is no doubt that the first genus must be considered as simply organized. The proofs for this are, in the first place, the structure of the cephalic end, which is of dactylogyrid-type; in the second place, the presence of one and not several testes; and in the third place, a more primitive structure of the uterus. However, the complete absence of the chitinous thorns, the presence of which we would have been justified to expect, on the cuticle in front of the attaching disc appears to be very strange. Hence it is possible that here occur certain secondary simplifications connected perhaps with the very small sizes of the worms which do not exceed 0.42 mm (Tagliani, 1912).

Sproston, (Sproston, 1946) transfers Enoplocotylinae from Acanthocotylidae into the family of Microbothriidae which, as is clear from comparison with the latter, cannot be considered in any way justifiable.

6. Family Microbothriidae Price, 1936.

Dermophagidae MacCallum, 1926; Labontidae MacCallum, 1927; Monocotylidae auct, part.

Worms of middle and large sizes with an oval, strongly flattened body. The posterior end is equipped with a very weakly developed cuticularized attaching disc which is deprived of chitinous hooks in the adult state. The p. 386 anterior end has a strongly developed musculature. On fixed subjects there is a weakly expressed false buccal sucker which perhaps is the result of the retraction of the anterior end during preservation. The eyes are absent. The intestinal system has a strongly developed pharynx and a two-branched intestinal tract forming more or less well-developed and branched lateral outgrowths; more rarely the trunks of the intestines lack outgrowths.

As a rule the intestinal trunks terminate blindly at the end of the body; as an exception in Pseudocotyle they merge with each other. The sex system has a common exterior opening of the sex atrium into which open the male sex organ and the uterus and sometimes also the opening of the paired vaginae. The male sex system has a single, double, or numerous testes and a copulatory organ equipped with a well-developed chitinous pipe which sometimes has a chitinous supporting apparatus. The female system has a rounded ovary, with well-developed vitellaria and a singular muscular vaginal duct; sometimes there are 2 vaginal ducts opening independently or into the genital atrium. The uterus is relatively short.

Parasites of the skin of Elasmobranchii.

Type genus, Microbothrium Olsson, 1869.

In addition to this, Dermophthirius MacCallum, 1926; Leptobothrium Gallien, 1937; Leptocotyle Monticelli, 1904; and Pseudocotyle Beneden and Hesse, 1865, enter into the composition of the family.

Limited material on adult and young individuals of Leptocotyle minor Monticelli collected from Scyliorhinus canicula (L.) from Naples (Mediterranean Sea) and from the same host from the Atlantic Ocean near England was at our disposal. The development of the species and also of other Microbothriidae is not known, which does not permit us to make reliable conclusions about the status of the family in this system. During special examination of our material, which was collected from preserved fishes with all possible care, we succeeded in substantiating the correctness of all previous researches in connection with the complete absence of chitinous hooks. Altogether the "sucker" of Leptocotyle gives a very strange impression. In spite of its relatively small dimensions the worms are very strongly attached to the skin of the host and it is difficult to remove them even in the preserved state. In the sections through the "sucker"[1] it is apparent that it has a relatively weakly developed musculature but contains a relatively large number of some sort of glands the ducts of which approach the inner surface of the cup of the "sucker," and apparently their secretions form a lining on the basic part of the above-mentioned surface which on the stained sections has the appearance of a black homogeneous plate. During removal of the worm by steam from the skin of host it is apparent that they are attached to the surface of a separate scale and that epibiasis (overgrowth, nobis) of the sucker of the worm by the tissues of the host is not observed. In such a fashion one can consider it certain that the attaching

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[1] At our disposal were two cross sections stained with iron hematoxylin. The worms were fixed on the body of the host in 4 % formalin.

disc of Microbothriidae acts differently than the one among all remaining Monogenoidea and represents a formation which serves for tight attachment to the body of the host. The attaching disc among *Udonella*, which was separated not long ago to an independent class of flatworms (Ivanov, 1952), has an analogous nature. This forces us to consider with great doubt the systematic status of the Microbothriidae. However, this does p. 387
not exhaust the peculiarities of the structure of this group. First of all, the coverings of the body are singular. Thus, in our preparations it is apparent that the cuticule has a very thin granular layer on its exterior surface which stains unevenly. It is difficult to say because of relatively poor fixation what the nature of this peculiarity is. A powerful layer of circular musculature which covers the entire body of the animal from the anterior end to the attaching disc without any interruptions is located under and tightly against the cuticule. We do not encounter any single species of monogenetic trematodes known to us which has such a distribution and thickness of the layer of circular musculature. As regards the internal organization and primarily the sex system, we do not observe any special peculiarity here with the exception that the copulatory organ and the vagina are equipped with a very powerful musculature which is very similar in structure to the circular musculature of the coverings. On the whole the sex system resembles the ones of the lowest monogenetic trematodes just as in many straight-intestined Turbellaria. As regards other genera of Microbothriidae we do not have any materials about their structure but judging by the literary data they basically resemble *Leptocotyle*. The isolation of *Pseudocotyle* into a special subfamily because of the presence of numerous testes in this genus is hardly supported and this genus apparently is very close to *Microbothrium* in which, although there is only one gonad, the testis consists of numerous follicles which, although united by a common connective tissue envelope, are separated from each other.

All in all, we can doubt the fact that Microbothriidae is a group belonging to the class of Monogenoidea. If subsequent research and primarily the study of the development of embryology shows the absence of the chitinous hooked armature of the attaching disc in all phases of development one may be able to speak with certainty that it is an independent group standing close to Rhabdocoela and perhaps even belonging to the order of Turbellaria. If it appears that this is not so and Microbothriidae are designated Monogenoidea then it will be more probable that they should be ascribed to Monopisthocotylinea to which they bear the greatest resemblance. Consequently until further studies we leave the present family in the group indicated as it is done in all contemporary résumés.

2. Order Tetraonchidea Bychowsky ord. nov.

Tetraonchinea Bychowsky, 1937.

Polyonchoinea, having larvae with 16 edge hooks on the attaching disc. Adult forms having an attaching armature consisting of 16 edge hooks, 1 - 2 pairs of middle hooks, and one connecting plate, which is sometimes absent (Tetraonchoididae). Sometimes there is supplementary armature in the shape of plates of varying forms. The copulatory organ has a chitinous pipe and a supporting apparatus. The cephalic end is of the dactylogyrid-type or with an undifferentiated glandular edge or it even forms 2 glandular lobes (Bothitrematidae). The digestive system has one intestinal trunk which does not have any lateral outgrowths; one family has 2 intestinal trunks terminating blindly (Amphibdellatidae).

Parasites of marine and fresh water Teleostei and marine Elasmobranchii.

Into the circle of this order belong 4 families--Tetraonchidae p. 388 Bychowsky, Amphibdellatidae (Carus) Bychowsky, emend., Tetraonchoididae Bychowsky, and Bothitrematidae Bychowsky, fam. nov.

During the study of monogenetic trematodes relative to Polyonchoinea after the publication of our work in 1937,we were forced to separate the families belonging to the suborder Tetraonchinea further from the rest of the Dactylogyridea and in this connection isolate them into a completely independent order. In spite of the considerable similarity of the lowest Tetraonchidea with Dactylogyridea,undoubtedly these groups are far removed from each other. As is clear from what has been said earlier, the Tetraonchidea have a very primitive characteristic--a large number of edge hooks in comparison with Dactylogyridea. As we have often indicated, the number of edge hooks is a very constant sign characterizing large groups of Monogenoidea and,as a result of this distinction by this characteristic alone,one should consider the representatives of Tetraonchidea as being far removed from the groups of species having the other number of them. With this,however, it is also characteristic that the edge hooks of Tetronchidea, in contrast to the large majority of the lowest Dactylogyridae, either do not grow at all or almost do not grow during the postembryonic period--this is an indication of considerable specialization and of the transfer of the function of attachment to other formations. Indeed, the characteristic tendency for Tetraonchidea is at first the strengthening of the role of the middle hooks and at the same time with a larger degree of co-ordination and then toward the transfer of the function of attachment to the disc itself. Although it is analogous to the one which we observe in Dactylogyridea this process takes place completely differently. This is seen in the case of the formation of the septa and of the secondary sucker-shaped pulvelli of Tetraonchoididae or in the characteristic strengthening of the disc in

Bothitrematidae. One cannot fail to note also that the pipe or sac-shaped structure of the intestine is characteristic for the majority of the families. There is no doubt that this is a very primitive characteristic which in this case has important significance and, as will be seen later, is encountered almost exclusively in Tetraonchidea. Unfortunately, the material at our disposal on the development (embryology) of the representatives of the present order was insufficient, but we can surmise that subsequent studies in this connection will show the correctness of our views.

1. Family Tetraonchidae Bychowsky, 1937

(Figs. 33, I, 64, 191, 192)

Tetraonchinae Monticelli, 1903, part.; Avielloidea Sproston, 1946.

Tetraonchidea having small or middle sizes in the adult state. The attaching apparatus of chitinous armature has 16 edge hooks, 2 pairs of middle hooks and 1 connecting plate consolidating all 4 middle hooks into one system. The intestinal tract is in the shape of a long single trunk without lateral outgrowths. The copulatory organ is chitinous consisting of a pipe and a single wavy plate supporting it. There are eyes. Other characters are similar to the ones among typical Dactylogyridae.

Parasites of fresh water and transitory Clupeiformes (Salmondei and Esocoidei). p. 389

Type and only genus, Tetraonchus Diesing, 1850.

This family was separated by us in 1937 from Dactylogyridae on the basis of differences in the number of edge hooks, different relations between the connecting plate and the middle hooks, and finally because of the presence of a one-trunked intestine, instead of a two-branched one as among Dactylogyridae. As regards the correlations between the middle hooks and the one connecting plate of Tetraonchus, such a type of formation of a simple, single four-hooked attaching system is absent among preceding families. The closest to this type is the nature of articulation of the hooks and of the two connecting plates among the genus Actinocleidus (Dactylogyridae, Ancyrocephalinae, see page 466). However, there are no bases whatsoever to suppose that the plate of Tetraonchus is the result of the merging of two and the existing similarity is, in such a fashion, only a coarse convergence. All this taken together enables us to consider it as fully justifiable to separate the family Tetraonchidae, in spite of the fact that in a number of characters they are very close to the typical four-hooked representatives of another order--Dactylogyridae. As a matter of fact, this similarity is fully understandable if we take into consideration the consanguinous relations between the two orders.

It is necessary to say a few words about the synoymy of the genus *Tetraonchus*. Omitting the fact that until recently this genus was confused with the genus *Ancyrocephalus*, now including representatives of the second in the first and now, conversely; one should not be surprised that until the present time the question about the independent existence of the "genera" *Dactylodiscus* Olsson, 1893 and *Aviella* Sproston, 1946 (=*Ancyrocotyle* Vlassenko, 1928) is still being discussed. Even in the beginning of the 20th century Monticelli in two of his works (Monticelli, 1903, 1905) indicates that the genus *Dactylodiscus* is synonymous to *Tetraonchus*; however, at the same time the author considered both *Ancyrocephalus* and *Amphibdella* as synonymous to the last genus, this did not sound convincing although it corresponded to the truth as will be shown later.

In 1937 in the résumé of Price the genus *Dactylodiscus* is left as a *genus inquirendum* with the indication that Johnston and Tiegs (Johnston and Tiegs, 1922) ascribed it as a subgenus to *Ancyrocephalus* without sufficient basis. In her résumé Sproston leaves *Dactylodiscus* without special examination indicating the opinions of the above-mentioned authors. Finally in 1952 in one of the works of Brinkmann (Brinkmann, 1952a) the author indicates that Nybelin found *D. borealis* Olsson (only species of the "genus") in Norway. One must point out that in 1928 Vlassenko described a new species and genus *Ancyrocotyle baicalense* (*sic*) which sharply differs from all the known forms of Monogenoidea by the presence of a primitive internal organization and a complex attaching disc with 6 suckers and 4 middle hooks. On the basis of the description of Vlassenko, Sproston separated the present form into a special family *Aviellidae*[1] in her résumé, establishing at the same time a special superfamily Avielloidea linking the last with Polystomoidea and Diclidophoroidea.

In 1934 we received from V. B. Dubinin material on Monogenoidea from *Thymallus thymallus* (L.) (typical host of *Dactylodiscus borealis*) from the river Pinega in the region of Archangel. During the study we succeeded in establishing that on it are representatives of the species described by Olsson and, at the same time, that this species is a typical representative of the genus *Tetraonchus*, i.e., the genus p. 390
Dactylodiscus has no right to existence and is synonymous to the first. Further, in 1936, having become interested in the "genus" *Ancyrocotyle* we collected material of this genus from the same host and from the same region from which the collections of Vlassenko were made and we explained

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[1] Sproston replaced the name of the genus given by Vlassenko which was a homonym of *Ancyrocotyle* Parona and Monticelli (*sic*), 1903 by *Aviella* Sproston.

that the mysterious form of *A. baikalense* is the same species as *T. borealis* Olsson. As regards the "suckers" on the disc of *Ancyrocotyle* it is true that during careless examination of individual specimens one can notice on the separate lobe-shaped outgrowths of the disc certain evaginations which resemble suckers but which actually have nothing to do with them, in connection with which the drawings and the description of Vlassenko are the result of a certain imagination because of an insufficient familiarity with the group. Unfortunately our data were not published,[1] which led to a certain regrettable error in the résumé of Sproston.

Finally, in 1948 Bauer published a special article in which on the basis of his, and especially our data, he indicates that *Ancyrocotyle baikalense* is equivalent to *Tetraonchus borealis*. One must note, however, that in this work he commits a number of errors based on a insufficient knowledge of the corresponding literature.

Thus, the question about the "genera" of *Dactylodiscus* and *Aviella* at the present time can be considered completely solved. One must also note that very recently a number of species of *Tetraonchus* from different Salmonidae and Thymallidae were described (Price, 1937; Bauer, 1948b; and others). However, because of considerable individual variability of the representatives of the present genus it seems probable to us that many of these species have no right to existence and possibly there is only one species, *T. monenteron*, which has different forms on different hosts. However, this supposition demands substantiation by statistical methods or even by experimental means.

2. Family Amphibdellatidae (Carus, 1885) Bychowsky *emend.*

(Figs. 284, 285)

Amphibdellidae Carus, 1885; Gyrodactylidae Cobbold, 1877, *part.*; Dactylogyridae, Bychowsky, 1933, *part.*; Tetraonchinae Monticelli, 1903, *part.*

Tetraonchidae, having small sizes in the adult state. Attaching apparatus consists of a chitinous armature with 16 edge hooks, 2 pairs of middle hooks and one connecting plate. Intestine with 2 trunks ending blindly, without lateral outgrowths. Copulatory organs chitinous, consisting of a pipe and a complex supporting apparatus. There are no eyes. Other characteristics as among Tetraonchidae.

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[1] The only reference to them is in the work of V. B. Dubinin (1936) where the author states that the genus *Dactylodiscus* is made synonymous with *Tetraonchus* and the species *D. borealis* Olsson is transferred into the latter.

Parasites of marine Elasmobranchii (Torpedinidae).

Type and only genus, *Amphibdella* Chatin, 1874, (Fig. 284).

In addition to the type genus a very close genus, *Amphibdelloides* Price, 1937, the independence of which cannot be confirmed on the basis of our data, was described.

To clarify the contradictory and inaccurate data of preceding authors we collected and examined considerable material from *Torpedo marmorata* Ris. and *T. ocellata* Raf. from the Mediterranean Sea (Bay of Naples) and the Atlantic Ocean (Bay of Arcachon), from *T. californica* Ayr. p. 391
from the Pacific Ocean (Shore of California) and from *T. smithi* S. from the Arabian Sea (near Beluchistan). First of all it was necessary to ascertain the true number of edge hooks of the attaching disc which are of principal significance. As is known, Chatin--the author of the genus *Amphibdella*, did not see the edge hooks at all. Parona and Perugia (Parona and Perugia, 1890b) indicated the presence of 6 pairs, Ruszkowski (Ruszkowski, 1931) found 8 pairs of them and in the résumés of Price and Sproston (Price, 1937b; Sproston, 1946) a new number is cited--7 pairs. Actually, as our verification confirmed, the number of edge hooks in *Amphibdella* is 8 pairs as was first indicated correctly by Ruszkowski and then confirmed by Palombi in his résumé of monogenetic trematodes of Italy (Palombi, 1949). Thus, the genus *Amphibdella*, by that characteristic alone, falls out of the family of Dactylogyridae to which it has been ascribed until the present time. The second uncertain question was the presence and the number of the connecting plates between the middle hooks of the disc. Thus, Chatin who described the genus does not indicate the presence of middle plates. Parona and Perugia in two important works published in the same year (Parona and Perugia, 1890a, 1890b) at first indicate the presence of one plate and give the corresponding drawing, and then speak about the presence of two plates among small specimens of *Amphibdella* showing this in a special drawing, and at the same time write that the larger samples do not have a single plate. Palombi (Palombi, 1949) confirms that the large individuals of *A. torpedinis* are deprived of connecting plates and smaller individuals have, according to his data, only one plate--which as a matter of fact he does not show. In a special note Palombi writes in addition to this that he examined the collections of Parona and not once did he find individuals with two connecting plates, although all the authors write that they are clearly and always visible among small worms. Price (Price, 1937b) divides the genus *Amphibdella* into two on the basis of the presence or absence of the connecting plates and also of the "lobed" or "unlobed"

nature of the disc and he separates a new genus *Amphibdelloides* which differs by the presence of the connecting plate in the disc which does not form any lobes in contrast to the genus which in his opinion is deprived of a connecting plate and has a disc with numerous "lobes." During the verification of considerable material it became clear that *Amphibdella* always has one connecting plate. Among younger samples it really is expressed more distinctly, whereas among older individuals it is relatively p. 392 poorly noticeable, especially in stained whole mounts. This plate is exceedingly thin and tender and apparently its relative growth is very weak so that in large specimens it has a rudimentary nature, so to speak. As regards the presence of the second plate which was indicated by Parona and Perugia, they mistook for it the transversal muscular band which connects the upper ends of the ventral pair of the middle hooks. This band is clearly apparent in a number of preparations and perhaps is really more easily noticeable among young individuals. Consequently, the character, presence or absence of the connecting plate which is basic for the division of *Amphibdella* into 2 genera by Price is not valid. Just as unimportant is the second sign--the formation of "lobes" on the disc. The so-called "lobes" actually are contractile portions of the body of the disc in which the hooks are located. Such outgrowths are formed on the bodies of practically all monogenetic trematodes during the attachment of the latter to the gills of the host, and appear, or disappear within strictly determined areas of the disc in connection with the constant distribution of edge hooks. One can note at the same time that during the preservation of younger individuals these outgrowths have already been removed by the worm before its death; whereas among the older ones they are affixed partially or fully in the elongated state. It is difficult to say what happens here but the slowing of the reaction to the fixing fluid is clearly shown in the individuals. As a matter of fact, this concerns not only the attaching disc but also the cephalic outgrowths as well as the general contraction of the body (it is understood during equal conditions of physiological "freshness" of the material). We also seem to see the same relation in *Amphibdella*. The younger individuals are more often fixed with retracted hooks and correspondingly the disc has a contracted shape (Fig. 285); whereas larger fixed specimens have more or less elongated shapes and the hooks are protruded further outside together with the adjacent sections of the disc itself (Fig. 285, B). However, the relative position of the hooks in both individuals is completely the same. The location of the "lobes" on the drawings of Ruszkowski and on the p. 393 figures of *A. flavolineata* in Price (Price, 1937b, Fig. 1) is approximately correct.

To the present time the internal structure of the representatives of the genus *Amphibdella* has also not been described very accurately. Thus Ruszkowski and subsequent authors represent the widening part of the seminal duct as a testis (=*vesicula seminalis externa*) whereas actually the testis lies behind the ovary and at any rate begins not higher than the middle of the flask-shaped part of the ovary. The fact that the testis is poorly visible on whole mounts is explained by its relatively small diameter. As a rule, the testis is rather long and contains an insignificant number of ripe spermatozoids, being basically filled with their earlier stages. In connection with this, it is apparent that there is strong development of the *vesicula seminalis externa*. The works indicated have inaccuracies in the expression and description of vitellaria, cephalic glands, *etc.* on which we are unable to dwell now.

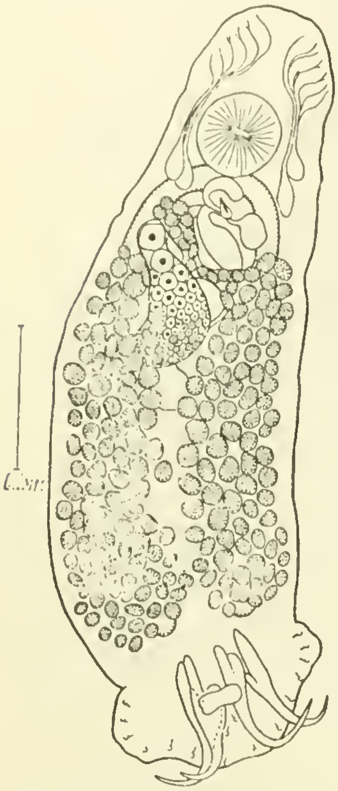

Fig. 284. *Amphibdella torpedinis* Chatin, adult worms from the gills of *Torpedo marmorata* Risso from the Basin of Arcachon (Atlantic Ocean).

Thus, so far only one genus, *Amphibdella*--synonymous to which is the genus *Amphibdelloides*--should be considered as having the right to exist and be considered in the composition of the family. The independence of the family was first indicated by Carus (Carus, 1885), however, clearly erroneously because he ascribed this family to the order Trematoda, suborder Digenea, having placed it together with the family of Amphillinidae in front of Monostomidae. After his work, no one paid any attention to this separation of *Amphibdella* into a separate family and ascribed this genus quite correctly for that time to the family of Gyrodactylidae, and later after the separation of the family of Dactylogyridae--to the latter. Nevertheless, at the present time there is basis for the re-establishment of the independence of the family, but for other reasons. As we have already indicated, the genus *Amphibdella* must be excluded from the suborder Dactylogyrinea and transferred to Tetraonchidea (*sic*). Within the limits of the last suborder this genus stands closest to the family Tetraonchidae. However, *Amphibdella* differs by a number of characteristics which do not permit it to be included in the present family and which force us to recognize the necessity of separating it into a separate family. The presence of the two-branched intestine in contrast to the one-branched intestine of Tetraonchidae should be considered as the first and most important characteristic. Taking into consideration the rarity among Monogenoidea of the one-branched intestine indicated above (see page 47) and the indubitable primitiveness of this characteristic, one should not unite the species which have one- and two-branched intestines[1] into one family. Further, even though the absence of the eyes is undoubtedly a secondary phenomenon among the majority of the Monogenoidea which have no eyes, nevertheless the presence of the given characteristic among Amphibdella hardly has the same nature, especially since we never did find a trace of eye pigment which usually occurs among a majority of other forms, even among the youngest individuals of the genus. It seems to us that for the present genus this is a more ancient characteristic underlying

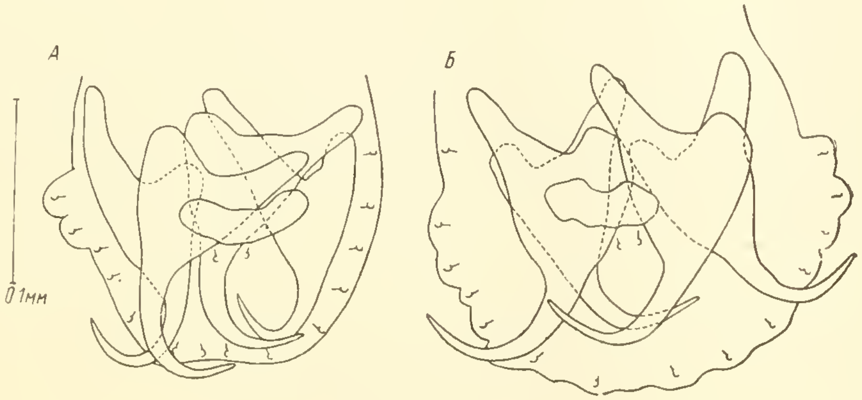

Fig. 285. Amphibdella torpedinis Chatin, attaching disc from the worms from the gills of Torpedo marmorata Risso from Arcachon Basin (Atlantic Ocean). A--of the young (but mature!) worms; B--of the adult worm.

its relatively old separation from other Monogenoidea. The latter also confirms, to a certain degree, the occurrence of Amphibdella on a group of very isolated hosts--electric skates. Although it was indicated by us in the diagnosis that the remaining basic characteristics of the family are similar to Tetraonchidae it is only true in general traits, but the separate traits of the structure of the cephalic and the copulatory organ, of the p. 394
vitellaria etc., also attests to the considerable peculiarity of Amphibdella. All this taken together forces us to consider the separation of this genus into an independent family as quite proper.

3. Family Tetraonçhoididae Bychowsky, 1951

(Fig. 29)

Tetraonchidea, having middle sizes in the adult state. The attaching apparatus consists of a sucker-shaped attaching disc having a chitinous armature consisting of 16 edge hooks, one pair of middle hooks and a special supporting plate lying near the central part of the disc; the

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[1] This remark does not pertain to certain of the highest Monogenoidea (see page 425).

middle plate is absent. In addition, on the dorsal side of the disc there are four symmetrically located, small sucker-shaped formations each with a cuticular thickening along one edge. The intestinal tract is in the shape of one trunk without lateral outgrowths. There are no eyes. The copulatory organ is chitinous with a strongly waving pipe and complex supporting apparatus. The remaining characteristics are just as among Tetraonchidae.

Parasites of marine Perciformes (Uranoscopidae).

Type and only genus Tetraonchoides, Bychowsky, 1951.

We have no special remarks at the present time concerning the present family because its description was given relatively recently (Bychowsky 1951). We shall only note as strange the fact that T. paradoxus Bychowsky, 1951 has not been found at the present time by any of the Italian researchers, although it exists in the Mediterranean Sea and apparently is widely distributed, because it was discovered in huge quantities on the only Uranscopus species examined by us in 1954 from the Bay of Naples (Italy).

4. Family Bothitrematidae Bychowsky, fam. nov.

(Figs. 19, 286, 287)

Bothitrematinae Price, 1936.

Tetraonchidea, having middle sizes in the adult state. The attaching apparatus consists of a sucker-shaped disc and its chitinous armature consisting of 16 edge hooks, 2 large middle hooks with a connecting plate and of a ring of pipe-shaped, flattened plates lying with their longitudinal axes along the radii, tightly against or almost adjacent to each other at a certain distance from the exterior edge of the disc. This ring of plates is interrupted on the anterior edge and at this place, but closer to the center of the disc is located a special coarse supporting plate similar to the one among Tetraonchoididae. The anterior end of the body has a pair of glandular cephalic lobes at the place of the cephalic glands of Tetraonchidae and 2 pairs of eyes of which the posterior one has a tendency towards merging. The intestine is in the shape of a single, sac-shaped trunk. The ovary is round, it is lying in front of the single testis. The vitellaria are strongly developed and fill the entire body from the pharynx to the attaching disc. The structure of the ducts of the sex system has not been studied. The copulatory organ is chitinous, pipe-shaped. The male sex opening is on the ventral side of the body.

Parasites of marine Pleuronectiformes (Bothidae).

Type and only genus, Bothitrema Price, 1936.

Price, who described the genus Bothitrema with the single species B. bothi (MacCallum 1913), separated it into a special subfamily Bothitrematinae relating it to Dactylogyridae. At the same time Price wrote that, "this species is an aberrant representative of Dactylogyridae, which is located between this family and Monocotylidae. The absence of lateral cephalic glands points towards its proximity to Monocotylidae, whereas the presence of a cuticular connecting plate between the middle hooks includes this form into the family (Dactylogyridae--B. B.)." We succeeded in explaining that, although the considerations of Price are p. 395

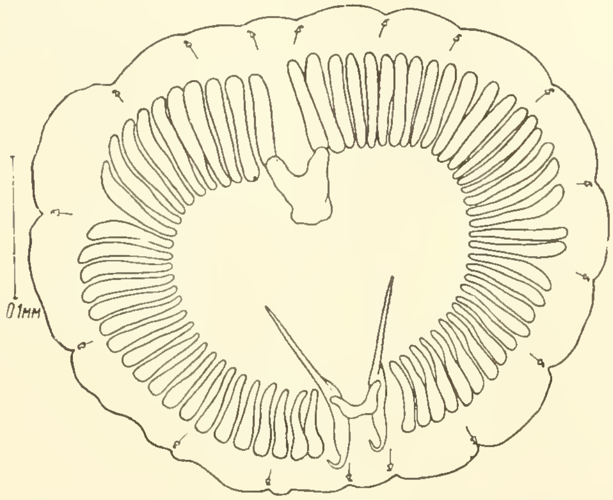

Fig. 286. Bothitrema bothi (MacCallum), chitinous armature of the attaching disc of an adult worm from the gills of Lophopsetta maculata (Mitch.) from the region of Woods Hole (Atlantic Ocean).

partially correct, nevertheless there are no bases whatsoever to ascribe D. bothii either to Dactylogyridae or to Monocotylidae, and this form is a representative of a special family relating to the order Tetraonchidae. First of all, in spite of the fact that during the redescription of D. bothii Price points to the presence in it of 14 edge hooks actually there are 16 of them (Fig. 286). Thus, the attribution of this species to Dactylogyridae is already incorrect. There are also a number of less important bases for separation of this form into a special family. Thus the structure of the attaching disc shows (Fig. 287) that it functions as a sucker and that the pipe-shaped plates constitute a supporting complex which gives the disc the ability to maintain a changing but relatively considerable depth. Judging by a number of specimens which were at our disposal and which were removed directly by us from the gills of the fishes (fixed), the basic role in attachment is fulfilled by the disc itself and only to a lesser degree by the middle hooks. As regards the edge hooks, they do not play any role at all in the attachment of adult forms or if they do play a role it is a minimal one. Thus, the attaching apparatus of Bothitrema functions differently than in Dactylogyridae and resembles, in its action, the one of the more highly organized groups--Calceostomatidae, Monocotylidae, Capsalidae and others. At the same time, because of the presence of a p. 396 ring of plates the disc begins to differentiate itself into two parts--the peripheral fringe and the "sucker" proper which is characteristic for Monocotylidae and which never occurs in Dactylogyridae. The plates of the disc themselves are neoplasms (new growths, *nobis*) which do not have any analogies in any other group of Monogenoidea. Inasmuch as these formations are of important adaptive significance, they should not be evaluated as a character of the second order. As regards the remaining chitinous armature, the presence of the connecting plate between the middle hooks, which undoubtedly resemble the one in Dactylogyridae, Tetraonchidae, and other close families--probably points to the homology of these formations. However, we do not have sufficient bases to consider it as a deciding significance, because the absence of this character in Tetraonchoididae, Monocotylidae and other families of the corresponding group is either a secondary phenomenon, i. e., a result of reduction, or, what is more likely, the consequence that the necessity for the strengthening of the system of the hooks during the development of the corresponding forms did not arise because of the short term of their functioning during the period of the individual life of the worms. The functional significance of the supplementary plate connected with the ring of the plates and located at the place of its interruption is not fully understandable. It is possible to think that it plays a certain role in the mechanical fixation of the upper edge of the disc, and also serves for the attachment of the musculature which extends into the disc from the body of the animal. Thus, this plate probably fulfills the same functions as the corresponding one in Tetraonchoididae. To say that it is homologous to the one of the latter would be very tempting, but without the materials on the development of both groups this cannot be confirmed. At any rate its presence forces us to consider more attentively the probable closeness of *Bothitrema* to Tetraonchoididae (see page 394).

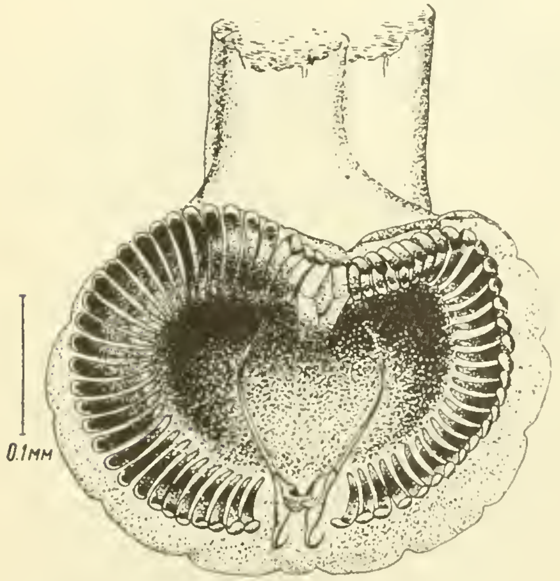

Fig. 287. *Bothitrema bothi* (MacCallum), general view of the attaching disc of an adult worm from the gills of *Lophopsetta maculata* (Mitch.) from the region of Woods Hole (Atlantic Ocean).

As regards the cephalic end of Bothitrema, according to the data of MacCallum (MacCallum, 1913a) and of Price--based on a few specimens which were collected by the first author,it has "head glands scattered in the pre-oral part of the body and has not gathered into lateral groups as among other representatives of the family (Dactylogyridae--B. B.) which (glands) open outside through 4 pairs of cup-shaped cephalic organs," (Price, 1937b). On the drawings in the works of both authors the cephalic end is actually represented with such cup-shaped depressions, more distinctly drawn in MacCallum's, and less distinctly in Price's. In our specimens, the structure of the anterior end is somewhat different (see Fig. 19). On p. 397 both sides of the cephalic end lie the thickened lobes which have a clearly glandular nature which resembles the one among the younger individuals of Nitzschia and even Benedenia. During the careful study of the lobes on our whole mounts we can see that they undoubtedly also have, in addition to glandular tissue, muscular tissue, apparently forming the depressions which were observed by MacCallum and Price and which are either not expressed at all or are hardly noticeable on some materials. Thus,one can suppose that the cephalic end of Bothitrema has a somewhat different type than the rest of Tetraonchidea and is close to the corresponding part of Monocotylidae and especially of certain Capsalidae. The internal organization of these interesting worms generally is not completely clear and,in this connection, we can hardly add anything to the data of Price. The elongated sac-shaped form of the intestine is important. In a small number of sections made from the middle part of the body of one worm (in the region of the ovary and of the testis) it is apparent that the intestine has two folds, that it is precisely sac-shaped and not pipe-shaped as in Tetraonchidae and Tetraonchoididae and in each trunk of the intestine of Dactylogyridae, Amphibdellatidae and others.

Thus,the basic traits of the structure of Bothitrema show that the genus cannot be included in the family Dactylogyridae as Price supposed and that it belongs to the circle of the order of Tetraonchidea in the first place, and in the second it should be isolated into a special family which is close to Tetraonchoididae, although it resembles the more highly organized groups in a number of characteristics, particularly representatives of Monopisthocotylinea from Dactylogyridea.

3. Order Gyrodactylidea Bychowsky 1937

Monopisthocotylea Odhner, 1912, part.; Polypisthocotylea Odhner, 1912, part.

Polyonchoinea having larvae with 16 edge hooks on the attaching disc. The attaching apparatus of the adult forms consists of a chitinous armature consisting of edge and middle hooks and often equipped with connecting plates. Among highly organized groups in addition to that there are 2 to 6 suckers on the attaching disc. The copulatory organ has a corona of chitinous hooks. The anterior end of the body has 2 groups of cephalic glands. The buccal opening often has a terminal sucker. The species which do not have suckers on the disc are viviparous, the rest egg-laying.

This order unites highly specialized species which are exemplified by live-bearing in part of them (Gyrodactylidae) and the parasitizing of Amphibia and Reptilia by the rest (Polystomatidae and Sphyranuridae). With this one must note as a very indicative phenomenon that the representatives of Gyrodactylidae and in particular, different Gyrodactylus--being typical parasites of fishes, are capable of parasitizing Amphibia; to be more specific, their larval stages--tadpoles (Stunkard and Dunihue, 1933; Pastukhova, 1950 and others). This can hardly be evaluated simply as a fortuitous occurrence of hosts of the first and the second groups!

The morphology of the larvae of Polystomatidae is unusually similar to that of young forms of Gyrodactylidae, but in the adult state they sharply differ in a number of relations. This is fully natural because the live-bearing habit, peculiar to Gyrodactylidae, places a distinct imprint on the entire organization of these worms. Within the limits of Polystomatidae and Spyranuridae, the common principle of structure appears very constant and one clearly observes the tendency toward the complication of the ducts of the sex system and the multiplication of the number of testes (see page 55). At the same time, the canalis genito-intestinalis, a formation connected with high productivity and higher tempo in the deposition of eggs, appears first among these families (see page 55). p. 398

The order consists of two suborders--Gyrodactylinea Bychowsky, and Polyopisthocotylinea (Odhner) Bychowsky.

1. Suborder Gyrodactylinea Bychowsky, 1937

Gyrodactylidea, predominantly of small sizes; viviparous. The young worms are born with a completely formed sex system. The attaching armature consists of 16 hooks, 2 middle hooks (the latter can be absent as an exception) and of a connecting apparatus. In connection with the latter sometimes there are supplementary chitinous formations which serve to support the disc in its open state. The anterior end has two cephalic outgrowths into which open the ducts of the glands. The eyes are absent. The digestive system with 2 intestinal trunks terminating blindly and not forming lateral outgrowths. The ovary is V-shaped; the testis is round.

Parasites of marine and freshwater Teleostei and cephalopods.

The suborder includes one family--Gyrodactylidae (Beneden and Hesse) Cobbold.

1. Family Gyrodactylidae (Beneden and Hesse, 1863) Cobbold, 1864

(Figs. 12, 32, E, 33, H, 43, 63, 131, 133, 134)

Gyrodactylides Beneden and Hesse, 1863.

The characteristics correspond to those of the suborder.

Type genus; *Gyrodactylus* Nordmann, 1832.

In addition to the type genus, *Icancistrum* Beauchamp, 1912; *Gyrodactyloides* Bychowsky, 1947; and *Paragyrodactylus* Gvosdev, 1953 enter into the composition of the family.

First of all one must note that we cannot agree with the interpretation of English researchers concerning the author who first established the present family. Price (Price, 1937b) indicates the family Gyrodactylidae with the name "Gobbold" (*sic*) and the year "1877." With this in the text he writes that "many authors including Johnston and Teigs (Johnston and Teigs, 1922), Fuhrmann (Fuhrmann, 1928), Froissant (Froissant, 1930), and Bychowsky, (Bychowsky, 1933c) relate the name of the family to van Beneden and Hesse (van Beneden and Hesse, 1863), whereas the latter authors gave the name "Gyrodactylides" and not "Gyrodactylidae"; the first which gave the correct form of the name of the family was Cobbold (Cobbold, 1877)." Sproston (Sproston, 1946) "corrects" the data of Price and indicates that for the first time the name Gyrodactylidae was used by Cobbold, not in 1877, but in the first edition of his book ("Entozoa: An Introduction to the Study of Helminthology...", 1864). It seems to us that such an attitude toward the establishment of the name of the author of the family is incorrect, formally and actually, In the work of van Beneden and Hesse it is clearly stated (van Beneden and Hesse, 1863, page 64) that the name "Gyrodactylides" is attached to a special family of trematodes and consequently these authors must be considered the first to establish the name of this family. All the supplementary changes in the spelling of p. 399
the name of this group without the changing of its rank should not in any way be considered as equivalent to authorship. Thus, Sproston correcting Price in the appellation of the subfamily Trochopodinae, indicates Price as its author and not herself (Price called this subfamily Trochopinae) which in our opinion is completely correct. However, an impression is formed that Anglo-American authors are sometimes excessively punctilious formally. (This remark is not limited to this present case.)

Within the limits of the family there is one monotypic genus--*Isancistrum*, which is encountered on squids and is characterized by the absence of middle hooks (Beauchamp, 1912). We can note in this connection that the indication of the presence of 15 edge hooks in *I. loliginis* Beauchamp is erroneous; there are undoubtedly 16 as among all Gyrodactylidae.

The genus *Isancistrum* is isolated by Fuhrmann (Fuhrmann, 1928) into a special subfamily--Isancistrinae, which is accepted in the subsequent résumés of Price (Price, 1937c), Sproston (Sproston, 1946) Dawes (Dawes, 1946) and others. Nevertheless we can consider, as was already indicated in our work in 1937, that such a separation is not in order because the absence of middle hooks cannot be considered as a characteristic differentiating the subfamily. This,in particular, concerns Gyrodactylidea in which,in the family Polystomatidae we see a considerable fluctuation in the number of middle hooks which at best is of generic importance taxonomically. The relation of *Isancistrum* and three other genera of the family is not clear. It is more probable that this genus is a derivative of *Gyrodactylus* which changed to parasitizing cephalopods and lost the middle hooks secondarily. As confirmation for this can serve the extreme rarity of the finding of Isancistrum and the absence of the finding of other representatives of Gyrodactylidae on cephalopods in spite of special searches which were conducted by us in 1946 in the region of southern Sakhalin.[1]

The interrelations of *Gyrodactylus*, *Gyrodactyloides*, and *Paragyrodactylus* are more clearly determined. Without any doubt, both last genera descended from *Gyrodactylus* - type ancestors independently of each other, and in both cases morphological complications proceed along the lines of acquisition of peculiarities (supplementary chitinous parts) of the attaching disc serving for the preservation of its constantly unfolded middle part. This peculiarity is undoubtedly a progressive one which permits a tighter and easier attachment of the worms to the body of their hosts and has an especially important significance in the cross-infection (transfer from one host to another, *nobis*) of the hosts (let us remember that the infection of the hosts takes place without the larva--by the adult worms).

2. Suborder Polyopisthocotylinea (Odhner, 1912) Bychowsky, 1937

Gyrodactylidea of middle and large sizes; egg-laying. The larvae have 16 edge hooks and often inceptions of the middle ones. Sometimes the larvae bear one pair of suckers in addition (Sphyranuridae). The adult worms have an attaching disc equipped with 2 or 6 muscular suckers and chitinous armature consisting of 16 edge and 1 - 2 pairs of middle hooks (which can be absent). The connecting apparatus of the p. 400

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[1] A certain number of squids examined by us in the Pacific Ocean in 1955 during the 22nd cruise of the expeditionary vessel "Vityaz" also were uninfected.

middle hooks is absent. The anterior end has weakly developed cephalic glands. The eyes usually exist--2 pairs. The digestive system has a more or less well-developed buccal sucker, powerful pharynx and 2 intestinal trunks often merging with each other at the posterior end. The intestinal trunks are simple or form external and internal branched outgrowths and sometimes even commisures which in turn give off more or less numerous outgrowths. The ovary is flask-shaped. The testes are single or numerous, more seldom there are 2 of them. There is a ductus genito-intestinalis.

Parasites of Amphibia and Reptilia and,as an exception, of aquatic mammals.

The suborder includes two families Polystomatidae (Carus) Gamble and Sphyranuridae Poche.

1. Family Polystomatidae (Carus, 1863) Gamble, 1896

(Figs. 22, 50, 62, 71, 73, 74, 77, 82, 83, 85, 91, 100, 101, G, 126-130, 203-215, 288, 289)

Polystomidae Carus, 1863.

Polyopisthocotylinea, having middle and large sizes in the adult state. The attaching disc bears 16 edge hooks, 0--2--4 middle hooks and 6 powerful suckers lying along the edge of the disc. Among adult worms the cephalic glands are strongly reduced and replaced by a buccal sucker. The eyes usually exist in the number of 2 pairs. The intestinal trunks are either simple, without outgrowths, or they merge at the posterior end either with outgrowths and also not merging at the posterior end or forming numerous outgrowths, several commisures and merging at the posterior end, with this a number of outgrowths departs from the place of the anestomosis. The ovary is flask-shaped, the testes are single or numerous, often follicular (see page 57), more rarely there are 2 testes. The uterus is either absent and the oötype contains one egg or there is a well-developed uterus.

Parasites of Amphibia and Reptilia, as an exception--Hippopotamus.

Type genus, Polystoma Zeder, 1800.

In addition to the type genus into the composition of the family enter Polystomoides, Ward, 1917; Parapolystoma Osaki, 1935; Diplorchis Osali, 1931; Polystomoidella, Price 1939; Neopolystoma Price, 1939; Oculotrema Stunkard, 1924; Protopolystoma Bychowsky gen. nov. [1] and, Eupolystoma Kam, 1850.

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[1] see page 280.

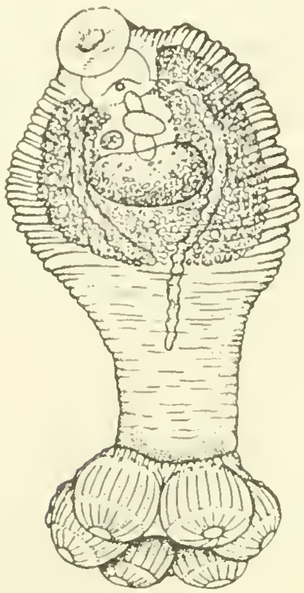


Fig. 288. *Oculotrema hippopotami* Stunkard, adult worm. Magnified 20 times. (According to Stundard, 1924).

The basic tendencies of the development of the family are obvious. Thus, we see a gradual complication of the digestive system from the simple 2-branched intestine, with trunks not merging at the end (*Polystomoides* and others) and then p. 401 the gradual appearance of outgrowths on the trunks (*Protopolystoma*), later the merging of the trunk at the posterior end (*Diplorchis*) and finally the appearance of interior outgrowths and anastomoses (*Polystoma*). At the same time, the process of complication of the sex system takes place. Among simply organized genera there is only one testis and there is no uterus in the real sense of the word; it is functionally replaced by an oötype containing one egg (*Polystomoides* and others). Further development proceeds along the lines of an increase in testes (*Diplorchis*--2 testes, *Polystoma*--follicular and numerous) and the elongation of the uterus (*Parapolystoma*, *Diplorchis* and *Polystoma*). The functional significance of these changes has already been noticed (see page 128). The processes of the progressive changes in the structure of the separate systems of organs do not coincide with each other and among *Parapolystoma*, for instance, we see only one testis but a very long uterus, with the presence of a more simply organized intestine. It is interesting to note that *Oculotrema*, parasitizing the eyes of the *Hippopotamus* (see however, page 219), has a rather primitive structure of the digestive and sex systems while it has a very powerful development of the attaching disc (Fig. 288). As regards the "primitiveness" of the sex system, this apparently is a secondary phenomenon, because in this genus the armature of the copulatory organs and the vaginal ducts are absent. These cannot be considered in this case as characteristics peculiar to ancestral forms.

2. Family Sphyranuridae Poche, 1925

(Figs. 35, 101, H, 216-219)

Dicotylidae Monticelli, 1903; Sphyranurinae Price, 1939.

Polyopisthocotylinea, of middle sizes. The attaching disc of the larvae and of the adult individuals bears 16 edge hooks, 2 middle hooks, and 2 powerful suckers. The anterior end has a large buccal suckers. The eyes are absent. The intestinal trunks are simple without outgrowths, they merge at the posterior end. The ovary is flask-shaped, the testes are numerous. The uterus is absent; the oötype contains one egg. Vaginal ducts are paired; they terminate blindly without opening outside.

Parasites of caudate Amphibia.

Type and only genus, *Sphyranura* Wright, 1879.

This family was first established by Monticelli (Monticelli, 1903) but he gave it a name which did not correspond to the name of the only genus which enters it, in connection with which, according to the rules of nomenclature Poche (Poche, 1925), completely correctly, gave the family its present name. Later Price (Price, 1939) transferred this family to the rank of a subfamily of Polystomatidae which, even though it was accepted by a number of subsequent authors including Sproston (Sproston, 1946), nevertheless cannot be considered correct. Just as in our work in 1937 we are completely in agreement with Poche that Sphyranuridae is an independent family for this is not only substantiated by the peculiarities of structure in the adult forms but also by features of the embryology, inasmuch as the differences between the larvae of Polystomatidae and Sphyranuridae are very important (see pages 186 and 190). It would be very tempting to consider Sphyranuridae as the more primitive group in comparison with Polystomatidae; however, the peculiarities of this group have a secondary nature, in connection with which the number of suckers of the attaching disc underwent indubitable oligomerization. One of the proofs of the origin of Sphyranuridae from *Polystome*-type ancestors is the presence of the closed vaginal ducts which play the role of peculiar p. 402
repositories of the sperm in this group just as is observed during the period of reproduction in *Polystoma integerrimum* Froelich, where the inflated part of the vaginal ducts is used for this purpose (see page 84).

Subclass Oligonchoinea Bychowsky, 1937.

Monogenoidea, having larvae with 10 edge hooks. As an exception the edge hooks can be considerably diminished in number (*Discocotyle*), or can even be completely absent (*Diplozoon*). In addition to the edge (hooks *nobis*), the larvae are equipped with 1 - 2 pairs of middle hooks and often with one pair of clamps of the same structure as in the adult animals. For the most part the larvae have one double eye, more seldom there are 2 pairs of them; often the eyes are completely absent. The attaching apparatus among the adults consists of metamorphosed suckers having valve structures (clamps) and equipped with chitinous apparatuses of different complexity. In the simplest cases the armature of these formations represents strongly developed edge hooks and in the most complex case--a system of chitinous parts forming the two hard valves of the pinching structure (clamps, nobis). The armature of the larvae is partially preserved on the disc of the adult animals or fully disappears through metamorphosis or by means of shedding. The cephalic end has 3 groups of glands. The buccal opening is subterminal and bears a well-developed sucker, or there are 2 special suckers in the buccal cavity which are not homologous to the suckers of the cephalic end of Polyonchoinea. As a rule, the eyes are absent among mature worms, very rarely they are preserved during the entire life (Diclybothrium).

Parasites of Elasmobranchii, Teleostomi (the large majority) and Holocephali. As an exception they are encountered on parasitic Isopoda. Thus, the representatives of this class have a narrower circle of hosts than Polyonchoinea; however, they are discovered on all groups of fishes on which the latter are also found.

The subclass comprises families relating to Polyopisthocotylea, according to the system of Price and Sproston, with the exception of Polystomatidae and Sphyranuridae which were ascribed to the preceding subclass on the basis of the data on their development and morphology.

The families which enter into the subclass are grouped on the basis of the structure of the attaching apparatus which has a tendency to greater and greater specialization of the ability to attach itself only to the gill filaments of a particular group of hosts. There are three main directions of change: 1) with the preservation and development of chitinous hooks in all stages of ontogenesis, the development of clamp-shaped suckers; 2) with the preservation of chitinous hooks without further development, the appearance of supporting elements in the clamp-shaped suckers; and 3) with the preservation or disappearance during the early stages of ontogenesis of chitinous hooks, the development of a larger or smaller number of real clamps bearing a complex system of supporting elements. For the last trend the appearance of asymmetry of the attaching apparatus and often of asymmetry and mirrorness of the attaching clamps themselves on the right and left sides is characteristic (clamps asymmetrical but repeated on both sides of the disk like mirror images, nobis). The peculiarities of the evolutionary development, which appears as a result of greater and greater adaptation to their hosts, lead very quickly to a complete or almost complete immobility of the representatives of the given suborder in contrast to what takes place in a majority of Polyonchoinea (see page 75). Just as in the preceding suborder we also observe a number of cases of converging p. 403 appearance of similar peculiarities here, the consideration of which is indispensable in the analyses of the true phylogenetic relations.

Into the composition of the subclass enter three orders--Diclybothriidea Bychowsky, Chimaericolidea (Brinkmann) Bychowsky, and Mazocraeidea Bychowsky.

1. Order Diclybothriidea Bychowsky, ord. nov.

Oligonchoinea having larvae with 10 edge hooks and 2 - 4 middle hooks on the attaching disc and with 4 eyes which can be absent (?). The attaching armature of the adult forms consists of 6 large, clamp-shaped suckers each armed with one strongly developed edge hook and of a varying number of unchanged edge hooks (capable of being completely absent) and of growing middle hooks located on the special finger-shaped lower part of the attaching disc. The latter can be equipped with a pair of fairly well-developed muscular suckers. The cephalic end has 2 lateral sucker-shaped pits not connected with the buccal opening, or the latter bears one more or less adoral sucker. The eyes among adult animals exist in the number of 4, or can be completely absent. The copulatory organ is equipped with chitinous hooks or is completely deprived of armature.

Parasites of Acipenseriformes and Elasmobranchii. Apparently as an exception they are encountered on Holocephali (see page 410).

The present order comprises very specialized forms in which the attaching apparatus bears obvious traces of secondary simplification. There is no doubt that the initial forms had an attaching disc equipped with 8 sucker-shaped clamps which was not differentiated into two distinctly separate parts--the disc proper and the offshoot. Proofs of this were cited by us in our common work with Gussew (Bychowsky and Gussew, 1950). To speak of the presence among contemporary forms of an "offshoot" of the disc is not correct, properly speaking, because it is the lower or posterior part of the attaching disc of the larva which grows weakly in the postembryonic period. On the other hand, its front or anterior part grows very strongly just as takes place in the secondary disc of Acanthocotyle. However, this is not a secondary disc but precisely the anterior part of the larval disc because the clamp-shaped suckers arising on it are incepted at the place of the location of the larval edge hooks (see 192 - 194). Hence it will be more correct to speak about the narrowed or widened part of the disc as was done in our work cited above.

Unfortunately, the development of one of the families--Hexabothriidae, has not been studied and consequently a number of questions about its systematic position remain unclear (see page 406). In connection with this, the small family-Diclybothriidae, which determines the name of this order, is taken as a typical family. In favor of this selection is also the fact that Hexabothriidae have a lower order of specialization than Diclybothriidae and thus are morphologically more singular than the latter (see, however, page 407).

This order includes 2 families which were united into one before our common work with Gussew. This formerly undivided family was ascribed to the superfamily Polystomatoidea Price, 1936, i.e., it was placed closer to forms which had a completely different origin and only convergent similarity with the group under discussion. This similarity was of a very coarse nature. Thus, the presence of the 6-suckered "disc" is common, but it was not taken into consideration that the 6-suckered condition p. 404 of Polystomatidae is a primary phenomenon, whereas the same number on the anterior, widened part of Diclybothriidea is secondary, and that the suckers of the latter are not homologous to the corresponding pairs of suckers of the former. Undoubtedly the location of the edge hooks in the suckers appears similar, but in the first place this phenomenon bears a more common nature and is not only encountered among these groups (see page 37), and in the second place the nature of the correlations between the hooks and the soft part of the suckers--clamps is different in both groups. Furthermore, if one considers the sex system, the latter has a different nature in Polystomatidae than among all the representatives of Oligonchoinea, as is apparent from what has been said before. One could consider the presence of the *ductus genito-intestinalis* as a rather important characteristic which links Polystomatidae to Diclybothriidea but as we have already indicated, this characteristic arises independently within the limits of both subclasses of monogenetic trematodes (see page 32). Strange as it may be, it seems to us that the most astonishing similarity is the unstable characteristic of the number of the eyes of the larva. Thus, in Polystomatidae (just as in the majority of Polyonchoinea) and among Diclybothriidea the larvae (and adults) are equipped with 2 pairs of eyes, whereas in the majority of Oligonchoinea usually there is only one double eye. As regards the larvae of Hexabothriidae it is more probable that they don't have any eyes at all, which, as is known, is not a rarity among larvae of monogenetic trematodes. Nevertheless the presence of 4 eyes points to the likelihood that this is a very ancient characteristic peculiar to common ancestors of both subclasses. As a whole, there are no bases to attribute important significance to this characteristic, taking into consideration the frequent reduction of eyes in a particular subclass, and the presence of 2 or even one merged eye in separate cases is found also in Polyonchoinea, and 4 eyes also among other Oligonchoinea (Microcotylidae, see page 214). Thus, all the characteristics common to Polystomatidae and Diclybothriidae are either primary or are actually convergent, to which one cannot attribute any significance which would liken these groups phylogenetically.

Two families--Diclybothriidae Bychowsky and Gussew and Hexabothriidae Price enter into the composition of the order.

1. Family Diclybothriidae Bychowsky and Gussew, 1950

(Figs. 51, 52, 90, 220, 221)

Diplobothriinae Monticelli, 1903; Diclybothriinae Price, 1936.

"Anterior end with two lateral sucker-shaped depressions not connected with the buccal opening (bothridia). There are two pairs of eye spots. The intestinal tract is 2-branched with lateral, exterior and interior outgrowths, the intestinal trunks merge at the posterior end of the body into the unpaired trunk extending into the middle or posterior end of the attaching disc. The unpaired trunk of the intestine can have lateral outgrowths, but it never extends into the posterior narrowed part of the attaching disc. The attaching disc has 3 pairs of clamps or suckers, inside of each of which lies one large chitinous hook. There is a more or less well-developed appendix (the narrowed part of the disc) which bears 3 pairs of relatively large and one pair of very small hooks and in a number of cases a rudimentary pair of suckers on the posterior part of the disc. The small hooks and the rudimentary suckers can often be seen only in live subjects or in serial sections."

"Parasites of sturgeon-types, Acipenseriformes, and Polyodontidae" (Bychowsky and Gussew, 1950).

Type genus, *Diclybothrium* Leuckhart, 1835.

In addition to the type genus there is also another--*Paradiclybothrium* Bychowsky and Gussew, 1950. p. 405

This family is characterized by very notable characteristics. The analysis which was conducted by us with Gussew (Bychowsky and Gussew, 1950) shows that in comparison with Hexabothriidae the representatives of both genera of Diclybothriidae are more specialized and the process of specialization is along the lines of the gradual disappearance of the attaching muscular formations, primarily during the time of its inception, with the preservation of all chitinous elements. Thus, in *Diclybothrium* the remnants of the first pair of suckers (suckers of the narrowed part of the disc) are also retained, whereas, *Paradiclybothrium* does not have them. At the same time further simplification in the structure of the attaching clamps of the widened part of the disc, which structually resemble the usual suckers more closely although this similarity is clearly of a convergent nature, also takes place in the last genus. Proofs of the fact that historically this process proceeded precisely in this fashion are on the one hand the peculiarities of the development of the chitinous elements of the disc and on the other, the details of the structure of the male sex system, particularly the presence of the bifurcation of the seminal duct and the penis of *Paradiclybothrium* which is deprived of chitinous armature. Let us also note that in the time which followed the publication of our work, *P. pacificum* Bychowsky and Gussew was discovered several times by us on its host from different regions from the Sea of Okhotsk.

As regards the justification of the separation of Diclybothriidae into an independent family, as we succeeded in showing with Gussew, the differences between this family and Hexabothriidae into which they were included are very important. Thus, although the attaching disc has a principal similarity in both families, the degree of the divergence between *Diclybothrium* and *Paradiclybothrium* on the one hand, and *Hexabothriidae s. str.* on the other--is very significant. As is apparent from the corresponding diagnoses, the structure of the anterior end in both families is different. There are also differences in the structure of the digestive and sex systems, although they are less important. Finally, the adult forms and probably also the larvae of both groups sharply differ by the presence of 4 eyes in Diclybothriidae and their complete absence in Hexabothriidae. Nevertheless, all this, as well as the parasitizing of different groups of hosts, which also confirms the importance of the divergence of both families, appears quite sufficient for the separation of the Diclybothriidae into an independent family.

2. Family Hexabothriidae Price, 1942

(Figs. 2, 36, 67, 101, I, N, 290-292)

Onchocotylinae Monticelli, 1903; Onchocotylidae Stiles and Hassal, 1908.

Diclybothriidea, having middle and large sizes in the adult stage. The attaching disc is subdivided into two parts--the anterior widened and the posterior narrowed,and having the shape of a more or less narrowed, mobile offshoot. The anterior part of the disc bears 6 clamp-shaped suckers, each equipped with a powerfully developed edge hook. The posterior part of the disc is equipped with 2 small muscular and relatively deep suckers and 2 middle hooks lying along the posterior edge of the disc between the suckers. In separate cases the middle hooks can be absent (?). The p. 406
anterior end has a more or less strongly developed preoral sucker. The eyes are absent. The intestine is two-branched with weakly branching lateral and middle outgrowths. The branches of the intestine merge at the posterior end of the body and form more or less well-developed ramifications in the disc,from which one extends into the narrowed part of the disc. The copulatory organ is equipped with chitinous hooks or more often is deprived of armature. The testes are numerous. The ovary is pipe-shaped, wavy, in front of the testes. The vaginal ducts are paired and open as a rule by 2 lateral apertures.

Parasites of Elasmobranchii and, as an exception, Holocephali.

Type genus, Hexabothrium Nordmann, 1840.

In addition to the type genus, Squalonchocotyle Cerfontaine, 1899; Rajonchocotyle, Cerfontaine, 1899; Rajonchocotyloides Price, 1940; Heteronchotyle Brooks, 1934; Pseudohexabothrium Brinkmann, 1952; and, Rhinobatonchocotyle Doran, 1953, enter into the composition of the family.

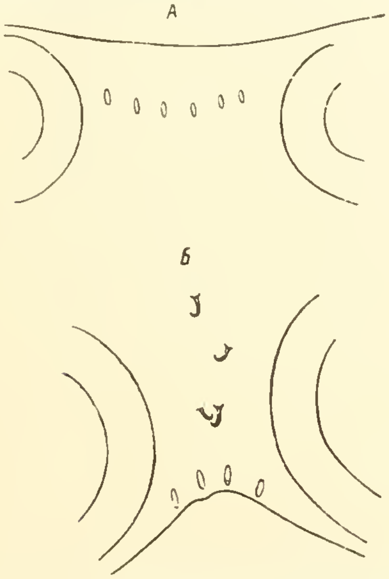


Fig. 289. Neopolystoma exhamatum Ozaki. A--Cuticular "button holes or loops" between the anterior suckers of the disc (edge hooks are absent!); B--Edge hooks and their "loops" between the posterior suckers of the disc (edge hooks lie separately from the "button holes or Loops!". (According to Ozaki, 1935).

As was mentioned before, the development of the worms of this family is completely unstudied and consequently we do not have any data about the larvae. In spite of that,one can attempt to visualize their structure on the basis of analysis of the peculiarities of adult worms. The question of the chitinous armature seems to be most interesting. As is known from what has been said before, the adult forms have 3 pairs of edge and one pair of middle hooks, with this the pair of suckers lying in the narrowed part of the disc lacks armature which represents an exception to all that is known to us of the correlations between the chitinous parts and the suckers. In his work, Cerfontaine draws attention to this and indicates that the anatomical structure of the large suckers which contain these hooks and of the small ones lying in the offshoot are very similar and even shows on a drawing of a section through the last place where the edge hooklet should have been "if it were there" (Cerfontaine 1900, Table XX, Fig. 6). For verification of the correctness of the observations on the structure of the attaching apparatus of Hexabothriidae, supposing that errors and the oversight of the very small chitinous hooks similar to the ones which were indicated in a number of preceding groups are possible, we especially studied live worms during our work at southern Sakhalin and the southern Kurile Islands (1946 and 1949). As a result,it appeared that besides the ones which are located in the 3 pairs of large suckers the edge hooks are actually absent, at any rate in those species of Rajonchocotyle and Squalonchotyle which we examined. However, in a number of individuals of different species of both genera we discovered, it is true with great difficulty, very interesting "remnants" of p. 407
2 pairs of edge hooks which appeared in the larvae. In a number of forms

(see page 28) the edge hooks have a special loop (Bychowsky calls it a buttonhole, *nobis*) through which the point of the hooks passes. In many Polystomatidae we easily observe these loops, and what is especially significant is that they often diverge (are displaced, *nobis*) from the hooks themselves and lie somewhat to the side of the latter. This phenomenon was observed not only by us but also by a number of other researchers. Thus, a number of drawings are reproduced in the works of Osaki to show this (Osaki, 1935a, Figs. 20, 25 and 26). Furthermore, Osaki writes that in *Polystomoides* (=*Neopolystoma*) *exhamatum* Osaki, 6 "loops" which sloughed off their edge hooks (Fig. 289) lie on the anterior end of the attaching disc between the anterior suckers. Thus instead of the normal 16 edge hooks which were in the larvae the adult individuals retain only 10 (4 lying on the posterior end and 6 in the suckers) having however, all 16 "loops." We observed the same picture of 2 pairs of "loops" of the edge hooks in a number of Hexabothriidae (Fig. 290). What is most interesting in this case is that one of these pairs was located in the small suckers approximately at the very same places where grown edge hooks lie in the large ones, i.e., fully corresponding to the suppositions of Cerfontaine! The second pairs of "loops" lies on the posterior edge of the disc near the pair of middle hooks, similar to what is observed in the larvae of Microcotylidae (see page 204). Hence, one can make the very probable conclusion that the larvae of Hexabothriidae have 10 pairs of edge hooks and one pair of middle hooks (the latter perhaps is incepted later), i.e., they differ in chitinous armature from the larvae of Diclybothriidae only by the absence of the second pair of middle hooks. As regards the remaining characteristics of the larvae, one can suppose that they are similar to the ones of *Diclybothrium*. The eyes constitute an exception about which we cannot say anything definite. It is more probable that they are either completely absent or have a different form than in *Diclybothrium* for if it

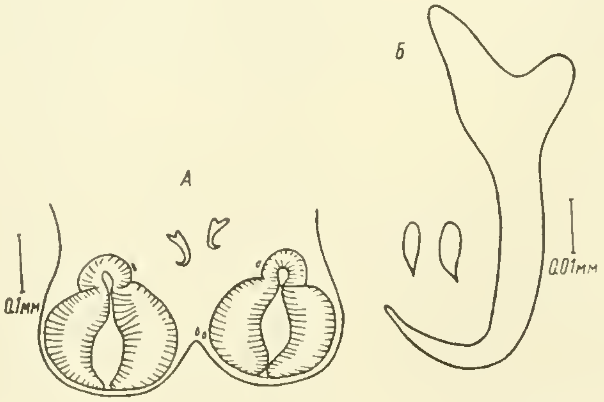


Fig. 290. *Squalonchocotyle* sp. from the gills of *Squalus acanthias* L. from the region of the Island of Shikotan (Kurile, shallow waters). A--Schematic drawing of the posterior end [of the "outgrowth" of the attaching disc (location of the "loops or buttonholes" of Bychowsky, *nobis*] ; B--Middle hook and "loops" of the same sample.

were not so we would have found some of their remnants. There is no basis to doubt our interpretation of the correlation of the chitinous and muscular attaching formations; consequently, also in connection with Hexabothriidae, one can firmly consider that just as in Diclybothriidae p. 408
their attaching disc is secondarily changed and appears to be derived from the 8-suckered and not the 6-suckered one as is the case in Polystomatidae. Taking into consideration the probability of the presence of a 10-hooked larva in Hexabothriidae their attribution to Oligonchoinea and particularly to Diclybothriidae cannot arouse any doubt.

Price (Price, 1942) divides Hexabothriidae *s. str.* into 2 subfamilies--Rajonchocotylinae and Hexabothriinae; however, this is undoubtedly erroneous, as Sproston correctly indicates (Sproston, 1946), not accepting this division in her résumé. The differences between the two basic genera of the family *Rajonchocotyle* and *Squalonchocotyle*, are so small that to give them the importance of subfamily characteristics is impossible. One should especially note also the fact that the morphology of the majority of the species of both genera is poorly studied and in a number of cases it is judged on the basis of the analogy with the structure of species studied in detail, mainly by Cerfontaine (Cerfontaine, 1896, 1900 and other works). The fact that this is so is indicated even by a superficial acquaintance with the literature. For instance, forms discovered on skates are attributed to the genus *Rajonchocotyle* and it is accepted that their internal structure corresponds to the typical species (*R. batis* Cerfontaine, *R. alba*, Cerfontaine and others), but it is impossible to judge either from the descriptions or from the drawings of the authors whether this is actually so (see for instance the descriptions and drawings of *R. wheri* Price, 1942 and *R. laevis* Price, 1942; for the latter species Price even indicates that the vaginal openings are not noticeable, to say nothing about the vaginal ducts themselves). However, our studies have shown that the attribution of a species to a particular genus on the basis of the characteristic of parasitizing sharks or skates cannot be permitted. Thus, for instance, at our disposal is a new and as yet undescribed species from a number of Far Eastern skates which has a very peculiar structure of the vaginal ducts, now uniting in front of the vitelline duct, now not uniting, and eggs with very long filaments and little feet (Fig. 291). Both these characters are differential for both genera and, furthermore, of the subfamilies of Price and pertain either to *Squalonchocotyle* (the vaginal ducts not uniting and eggs with filaments and little feet) or *Rajonchocotyle* (vaginal ducts which unite). Thus, the same species which is found in large quantities possesses characteristics of both genera and subfamilies. For us its true generic affinity is not important at the present time but what has been said expresses the danger of classification according to the host and also the impossibility of separating subfamilies on the basis of the characters accepted by Price.

The relations of the genera within the family are not quite clear. One can suppose, however, that the absence of the chitinous armature of the

copulatory organ in a majority of genera is a secondary phenomenon, and consequently Hexabothrium is a more ancient species. Further, it is quite probable that Heteronchocotyle conversely is a younger genus and the alteration of its attaching disc is a secondary phenomenon. The last genus deserves special attention because the structure of its disc provokes a number of important considerations. First of all the drawings of the author (Brooks, 1934) and Price (Price, 1942) hardly reflect the true relationships between the parts of the attaching disc (Fig. 292, A). Actually it is probably symmetrical and has a shape which is similar to the one drawn in Fig. 292, B. From this drawing it is apparent that the largest hooks are the ones lying in the posterior-most pair of suckers, following according to size--one located in one of the middle suckers and the smallest ones in one of the middle and two of the upper suckers. Similar correlations p. 409
resemble very much the picture observed in the growth of the larvae of Diclybothriidae during the postembryonic period and is analogous to what takes place during the growth of the larvae of Microcotyle, Diplozoon and so forth. The difference in the sizes of the hooks of the middle suckers cannot play a principal role because the similar pictures of asynchronous growth of the chitinous elements of the right and left halves of the disc are

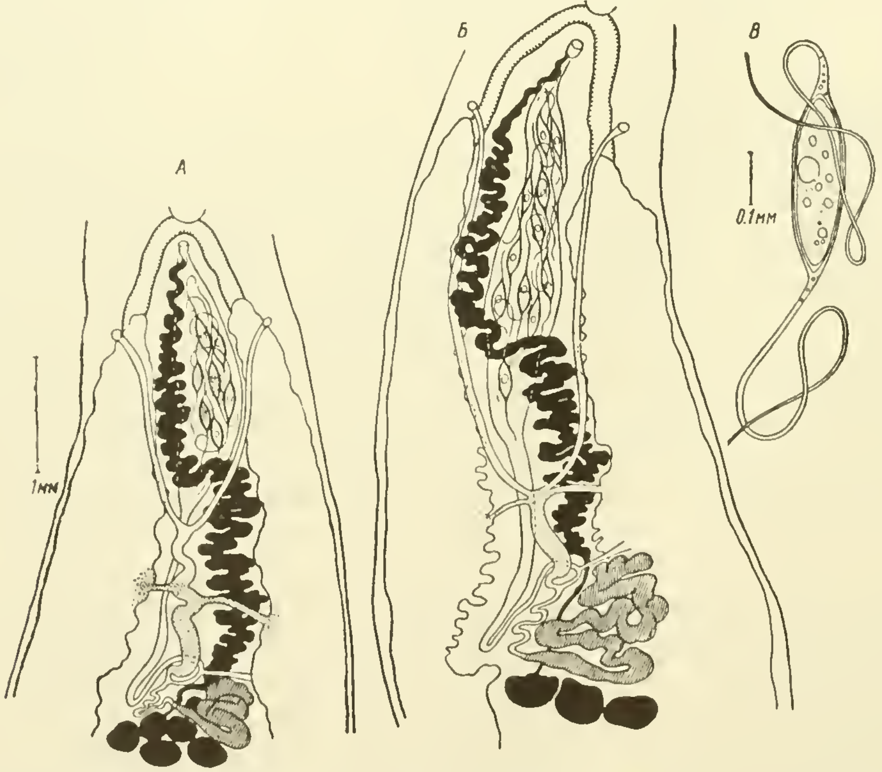
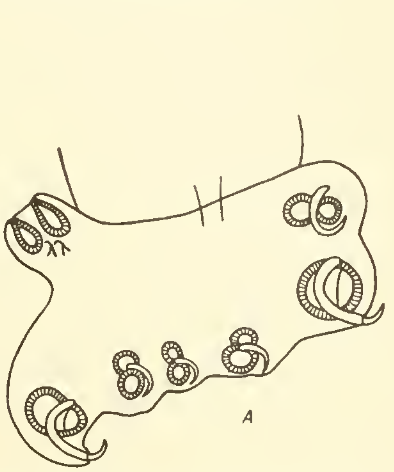


Fig. 291. Hexabothriidae (gen. et sp. nov.) from the gills of Raja rosispinus G. and Town, from the region of the western shore of S. Sakhalin (Sea of Okhotsk). A--The section of the body of the individual with a sex complex (vaginal ducts start with a common trunk!); B--The section of the body of an individual sex complex (each of the vaginal ducts begins independently!); C--Egg (filament and little foot!).

encountered very often among different Monogenoidea. Hence, we can conclude that either Heteronchocotyle does not represent an independent genus but only a stage in the development of some sort of species of Hexabothriidae of typical structure, or else the "formation" of this genus took place by way of reaching maturity during a delay in the one of the stages of post-embryonic development. As is known, such a type of evolutionary development is appraised at the present time as being very progressive and occurring sufficiently frequently in different groups. It will be possible to make final conclusions about the independence of Heterochocotyle only after special studies. However, for the time being we consider the preservation of this genus more correct.



p. 410

Fig. 292. Heteronchocotyle hypoprioni Brooks, attaching disc of a worm. A--According to Brooks, 1934; B--Diagram of the supposed structure.

As regards the remaining 4 genera it is most probable that Squalonchocotyle, in which more simple relations between the vaginal and the vitelline ducts occur, is the most primitive. It is indispensable to note that during the examination of a preserved sample of Callorhynchus antarcticus Lacepede from Australia obtained in 1884 (collection of Z. I. N. Acadecmy of Sciences SSSR, No. 7052) we discovered one damaged specimen of a monogenetic trematode undoubtedly related to Hexabothriidae and apparently to the genus Squalonchotyle. Thus, we can consider that even though they occur very rarely,[1] nevertheless, Hexabothriidae are encountered on Holocephali.

2. Order Chimaericolidea (Brinkmann, 1952)
Bychowsky ord, nov.[2]

Oligonchoinea, the development of which has not been studied but probably having larvae with 10 edge and 2 to 4 middle (?) hooks. Adult forms of large sizes. Their attaching disc is delimited from the body by a long "stem" devoid of sex ducts and glands. The armature of the disc consists of one pair of edge and 2 pairs of middle hooks and 4 pairs of more or less equal clamps each equipped with 3 chitinous parenthesis-shaped sclerites. The cephalic end bears a weakly expressed buccal pseudosucker, or is even deprived of it. The eyes are absent. The intestinal system has a small pharynx and a rather long undivided anterior section of the intestine which divides into 2 trunks somewhat behind the vaginal apertures which form weakly developed external and internal outgrowths and which p. 411 extend posteriorly up to the attaching disc in which they end blindly without merging. There is a common sex aperture into which open the orifaces of the uterus and the male copulatory organ, which is equipped with chitinous thorns or is free of them. The testes are numerous. The ovary is branched; it is single or double. The vaginal ducts are double. They open along the sides of the body somewhat behind the common sex atrium. The uterus is strongly developed; it is sac- or pipe-shaped. The vitellaria lie along the sides of the body starting from the level of the pharynx and terminating without extending into the "stem" of the attaching disc.

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[1] Until now, in spite of the rather numerous dissections of Chimaera, only representatives of the family Chimaeracolidae have been discovered on them.

[2] In 1952 Brinkmann isolated the superfamily Chimaericolidea to which we attribute the status of an independent order.

Parasites of Holocephali.

Contains a single family, Chimaericolidae Brinkmann.

The comparison of the structure of the representatives of this order (see below) and that of Diclybothriidae points to their considerable similarity; however, sharp differences in the structure of the sex system as well as different orientations and tendencies of development of both groups do not permit these groups to be united into one.

1. Family Chimaericolidae Brinkmann, 1942

(Figs. 53, 101, K, 107, 293-296)

The characteristics correspond to the characteristics of the order.

Type genus, Chimaericola Brinkmann, 1942.

In addition to the type genus, Chimaericolidae also contains one other genus, Callorhynchicola Brinkmann, 1942.

The structure of the representatives of the present family is very unusual and is of considerable theoretical interest. First of all it is indispensable to dwell on the structure of the attaching apparatus and in particular on the clamps. The latter are described sufficiently accurately and in detail by Brinkmann (Brinkmann, 1942b). However, a number of the important details and peculiarities did not attract the attention of this very meticulous researcher. As material for the analysis of the present structure, we had a certain number of individuals of Chimaericola leptogaster (Leuckart) gathered from Chimaera monstrosa (L.) from the regions of the Norwegian Sea adjacent to the shores of Norway, i.e., of the very same source as the material of Brinkmann and, in addition to that, one example of a second species of Chimaericola from the gills of Chimaera colliei Lay and Bennett from the Pacific Ocean near the shores of San Francisco which has not yet been described.

The normal clamp of Chimaericola has the appearance of a cup-shaped formation, flattened in the dorsoventral direction and lying on a special outgrowth of the attaching disc. In relation to the disc, the clamps are oriented in such a way on its ventral surface that they constitute two mirror-like rows similar to each other, the right and left containing four clamps each of more or less the same size. Together with the mirrorness (bilateral symmetry, nobis) of the location (Fig. 293) the clamps of the right and left sides are "mirrored" (bilaterally symmetrical, nobis) in the structure and correlation of the separate parts which comprise them, and essentially do not differ in any way from each other. The separate clamp (Fig. 294) is shown in the open state which practically is never encountered and can be obtained only artificially. It has the shape of an almost regular, rounded cup the circumference of which bears 4 invaginations along the two perpendicular diameters--2 along the sides of the clamp on the right and left sides and 2 correspondingly on the front and back. These depressions are formed in the first place by the soft parts of the clamp and particularly by the thickened edges (lobes) of the musculature. With this, the anterior right and left lobes are completely interrupted between each other and are separated from the posterior ones, whereas the latter, properly speaking, represents a single lobe which is merely curved in the middle.

Thus, in the natural state the clamp is bent in half in such a way that its first half becomes the anterior valve of the clamp and the second--the posterior, so that we can accept that there exist right and left lobes of the anterior and a united lobe of the posterior valves. A middle chitinous "parenthesis" lies along the line (the midline, nobis) of the clamp in such a fashion that its anterior end reaches to the anterior edge of the clamp and slightly protrudes outside between the right and left lobes. The basal part of the "parenthesis" follows the curvature of the valves of the clamp and its posterior end is located within the body of the posterior valve, somewhat short of its free end. On the unfolded clamp it is clearly apparent that two other chitinous "parentheses" lie to the right and to the left of the longitudinal axis of the clamp in direct proximity with p. 412
the edge lobes curving approximately in parallel fashion to their curvature and forming, in such a fashion, 2 chitinous bows--right and left. With this, their larger part is located in the anterior valve where they come closer to the middle parentheses and to the middle of the anterior edge. As regards the posterior parts of the parentheses they are further away from the edge lobe (posterior edge?, nobis) and their ends are considerably further removed from each other. On the closed clamp, i.e., on the clamp which is in its normal state, both of these "parentheses" occupy the position in the perpendicular plane in relation to the plane of the middle "parenthesis." Thus, the clamp acquires skeletal support which gives it a

framework on the periphery of the clamp for opening and also controlling its depth.

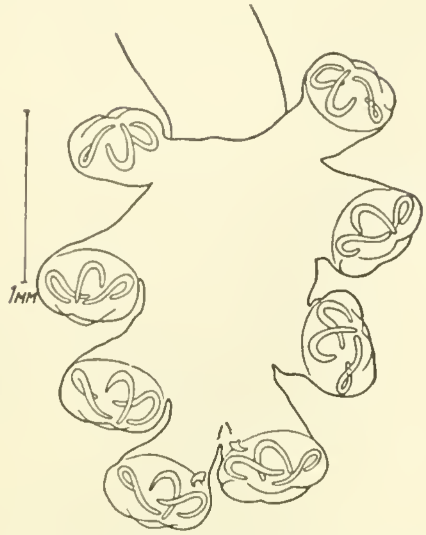

Fig. 293. Chimaericola leptogaster (Leuckart), attaching disc of an adult worm from the gills of Chimaera monstrosa L. from the Norwegian Sea near the Island of Sere.

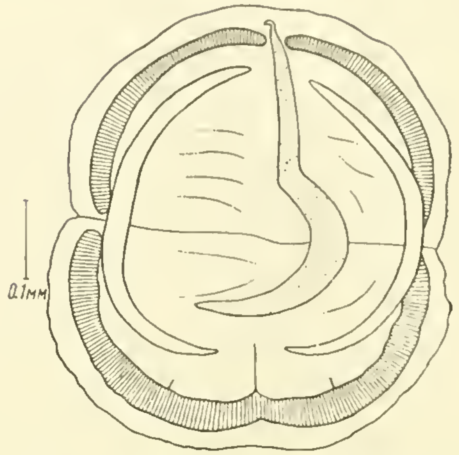

Fig. 294. Chimaericola leptogaster (Leuckart), artifically unfolded clamp. The musculature is represented by cross-hatchings.

Without speaking for the time being about the peculiarities of the "parentheses" we shall indicate that they are undoubtedly very resilient formations (we have verified this by direct experiments on other species of p. 413
Oligonchoinea), which seek to straighten themselves out, it is true within the limits of their normal curvature, so to speak. Hence, it is clear that the movement of the clamp, as has already been said before (see page 31), takes place during closing with the help of musculature which draws the valves together and which bends the "parentheses" and during the opening, thanks to the resilience of the latter, returning to their initial state and at the same time moving the valves apart. All in all,the chitinous parentheses have a double function--moving and supporting at the same time. As regards the latter function, in addition to "parentheses" it is also borne by the thin subcuticular membrane delimiting the clamp both from the exterior (the thinner) just as from the interior (thicker) sides and forming a noticeable cross-hatching of the surface of the clamps similar to the one in Diclybothriidae (Bychowsky and Gussew, 1950) but more tender. This subcuticular lining of the interior surface of the clamps forms a clearly noticeable edge seam which in preparations produces an impression as if it were lying under the muscular lobes. Along with this, on the anterior valve this seam forms three furrows, one of which extends to the posterior end of the middle "parenthesis" and two lie approximately along the middle of each half of the posterior lobe of the musculature. Similarly, also, on the anterior valve there is a larger seam into which enters the anterior end of the

middle "parenthesis". The precise structure of these seams is not clear because we did not have sections of suckers of *Chimaericola*; however, judging by analogy from *Diclybothrium* these seams represent the place where the membranes of the right and left halves of each valve join, because the subcuticular membranes of the disc is not a single whole but consists apparently of two separate parts representing sheaths so to speak, covering each half of both valves on all sides. This is not altogether accurate and it is possible that there are not two sheaves but even four. It is clear from the above-mentioned that even in such a primitive form as *Chimaericola* the clamp is a very complex formation differing considerably not only in its function but also in its peculiarities of morphological structure from the suckers peculiar to Polyonchoinea.

Very important is the question concerning the chitinous "parentheses" of the clamp, their structure and origin. If this question has already been discussed in general traits (see page 32), on the other hand, for Chimaericolidae it represents particular but nevertheless important interests. During the examination of all three parentheses, the first thing that jumps to the eyes is the completely different "facteur" (make-up or structure, *nobis*) of these formations. Thus, the middle "parenthesis" is homogeneous and produces the impression of being very dense and compact, whereas both lateral parentheses have a different structure, but with greater numbers of slit-shaped depressions located along their interior surfaces and they appear to be more frail in spite of their considerable sizes, It is noteworthy that in a number of cases in glycerin-jelly preparations which we have of the clamps it is clear that they have a yellow color, whereas the middle "parenthesis" is absolutely white. As regards the middle "parentheses" its shape in the extreme resembles the one of the hooks of the clamp of Diclybothriidae. Thus, even during careful examination of the anterior end of this "parenthesis," which is very sharpened in comparison to the rounded and thickened posterior end, one can often notice a more or less distinctly expressed hook-shaped curvature corresponding to the edge or point of the hook of Diclybothriidae. This is seen especially distinctly on preparations of younger samples of *Ch. leptogaster* Leuckart and on the only individual of the new species. The ends of both lateral parentheses have a completely different character; as a rule they gradually narrow and terminate in a p. 414
more or less rounded form, and at the same time each is alike at both ends. Hence, one can consider, it seems to us with a great degree of probability, that the middle "parenthesis" and the edge ones have a different origin in the first place, and in the second place that the middle parentheses of the clamps of Chimaericolidae are homologous to hooks of the suckers of Diclybothriidae and consequently represent strongly altered edge hooks of monogenetic trematodes. Unfortunately, until additional material on the development of Chimaericolidae is obtained, the last conclusion, probable as it may be, nevertheless remains conjectural. However, one can say that the attaching clamp of Chimaericolidea and Diclybothriidea are the most primitive in the group Oligonchoinea. In

spite of the fact that the clamps of the second have only the middle hooks and the first have two lateral "parentheses" in addition one should recognize Chimaericolidea as the more primitive group because they have 8 more or less developed clamps whereas among Diclybothriidea we already see the process of the subsequent reduction of the posterior (ontogenetically first) pair of clamps which extends very far in separate cases. As confirmation of this conclusion we can find a number of other peculiarities of Chimaericolidea. Thus first of all, attention is attracted by the structure of the cephalic end. In contrast to the majority of Oligonchoinea just as in the basic mass of the genera of Diclybothriidea in Chimaericolidea there are no traces of the inception of two suckers of the buccal cavity (Fig. 53). Their rather large buccal cavity opens outside on the ventral side, somewhat away from the anterior edge of the cephalic end. The buccal opening has a weakly muscular surrounding lobe which, although sometimes acquiring a sucker-shaped form it nevertheless is not separated by a special membrane. The anterior end of the body does not form any outgrowths and the existing, p. 415
relatively weakly developed head glands open evenly along the entire anterior edge. All this taken together represents characteristics again more primitive in comparison with peculiarities of the cephalic end of Diclybothriidea. Exceedingly singular and phylogenetically very interesting is the structure of the ovary in both known genera of Chimaericolidae. In Chimaricola according to the description of Brinkmann (Brinkmann, 1942b) the ovary is not compact but consists of a number of elongated folliculi of different

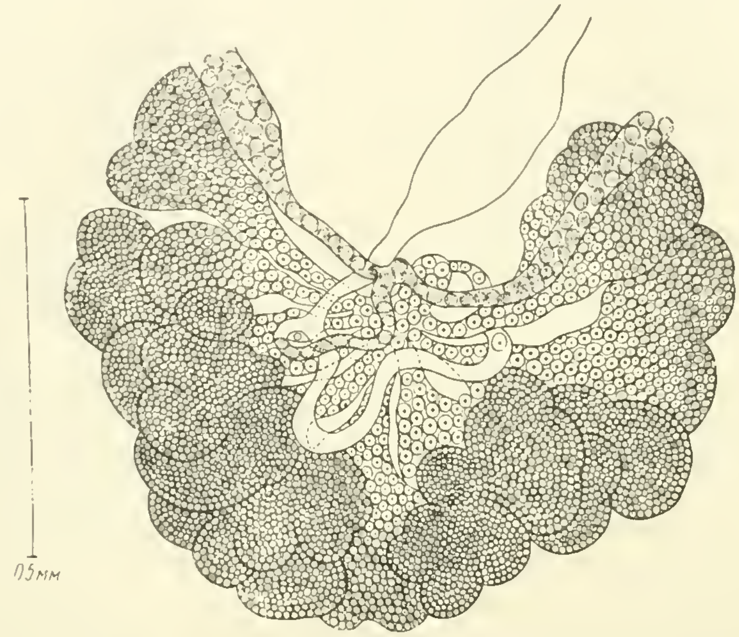

Fig. 295. Chimaericola leptogaster (Leuckart), the ovary of an adult worm from the gills of Chimaera monstrosa L. from the Norwegian Sea near the Island of Sere.

sizes in contrast to the other Monogenoidea. These folliculi merge into a common anterior transverse commisure which partially changes into an oviduct at its middle part. These data are basically substantiated during the examination of strongly compressed samples; however, the description of Brinkmann should be somewhat supplemented. Thus, first of all one must say that the ovary of Chimaericola (Fig. 295) consists of numerous, completely independent, separate parts (folliculi) each of which has a widened mace-shaped chamber, often with several curvatures and a more or less elongated canal—little pipe. Stages of development of the egg cells take place in the chamber of a separate follicle, already fully-ripened oöcytes ("which have cut themselves out" see page 84) are located in the canal. All the ducts of the separate folliculi, often joining in pairs, lead to the middle of the body where they merge into a common, more or less rounded "oöcyte-receiver" from which the oviduct emerges. There is no special transverse commisure of the ovary at all. It is apparently an erroneous interpretation of pictures observed in cross section. It is most probable that Brinkmann mistook part of the "little pipes" of the ovarian folliculi for this commisure. We were not able to count the number of folliculi; on the drawing of Brinkmann, the number of lobes (folliculi) equals 12. In our preparations it is apparent that the minimum number of little pipes is 15, and consequently there are no fewer folliculi. Among Callorhychicola [according to the description of Brinkmann (Brinkmann, 1952a)] the ovary is similarly arranged (Fig. 296), but consists of two groups of folliculi with independent oviducts merging together afterwards. With this, one of the groups (the right) is much smaller than the other and a smaller number of separate folliculi comprise it. Similar structure of the ovary is very rarely encountered among monogenetic trematodes. Thus, the ovary in Capsalidae (see page p. 416
475) is similar, although it is more coarsely arranged, and it is probable that something similar exists also in Loimoidae (see page 370). On the other hand, the similarity in the structure of the ovary in Chimaerichola and Callorhynchicola with the ones among Gyrocotyloidea and tapeworms (see page 475) is very important. Now we must say that the present

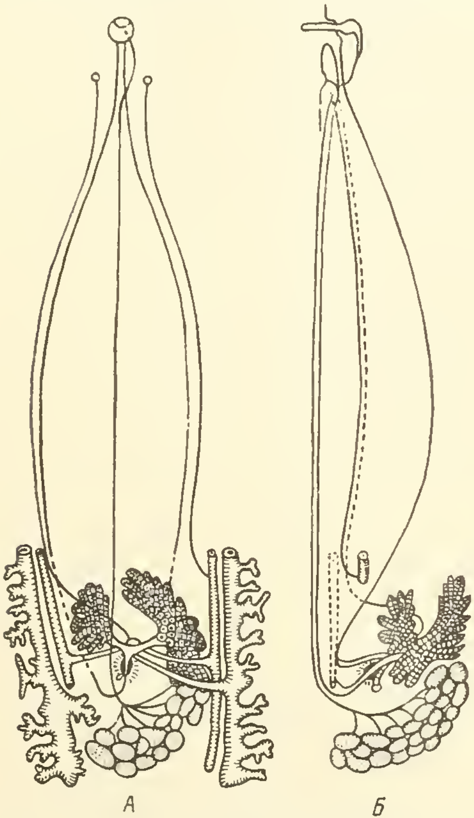

Fig. 296. Callorhynchicola branchialis Brinkmann, the diagram of the sex system from the ventral side (A) and from the side (B). (According to Brinkmann, 1952).

structure of the ovary in Chimaericolidae should hardly be considered as a secondary phenomenon because we also observe similar pictures among Turbellaria.

Without dwelling on a number of other peculiarities of the anatomy of Chimaericolidae we can say that as a whole this family possesses a number of very primitive peculiarities along with the very advanced specialization which was clearly expressed. As we will see further, this conclusion has important meaning for an understanding of the correlations of the evolutionary ways of development of the given group (see page 449).

3. Order Mazocraeidea Bychowsky, ord. nov.

Diclidophoroidea Price, 1936; Dactylocotyloidea Brinkmann, 1942.

Oligonchoinea, having larvae with 10 edge and 4 middle hooks on the attaching disc. As an exception, the number of edge and middle hooks can be smaller and also the clamps can appear at the place of one pair of edge hooks in the embryonic period. The attaching armature of the adult forms consists of more or less typical clamps numbering from 4 to several tens of pairs. Sometimes the number of the clamps is smaller and they develop only on one side of the disc. The larval armature partially remains during the entire life, and the anterior edge hooks enter, changing their shape, into the composition of the chitinous elements of the clamps and in a number of cases disappear, predominantly by means of a casting off of the posterior part of the disc and of the pair of edge hooks and two pairs of middle hooks which are located in it. The cephalic end has three more or less developed groups of glands. The buccal opening is terminal or subterminal. Its cavity is equipped with 2 muscular suckers, not homologous to the cephalic suckers of Polyonchoinea. The eyes are absent among adult forms; among larvae they are either absent or there is one pair of eyes usually merged; more seldom there are 2 pairs. The digestive system has a pharynx, usually a short esophagus and two intestinal trunks terminating blindly or merging. As a rule the trunks of the intestine have numerous lateral outgrowths which also anastomose with each other, in connection with which the intestine often assumes a net-shape. Mostly there is a common sex atrium often armed by various thorns. The armed or unarmed copulatory organ opens into the atrium. The testes are more or less numerous, more seldom there is one testis. The ovary is usually strongly curved with a flask-shaped oögonial chamber. The vaginal ducts are double or single, they open by one or two apertures often armed by chitinous hooks. The uterus is strongly developed, it is often sac-shaped. The vitellaria are strongly developed, they lie along the sides of the body.

Parasites of marine and, more rarely, fresh water Teleostei. They are encountered mainly on Perciformes. In separate cases they are known from parasitic Isopoda.

This order is subdivided into Mazocraeinea Bychowsky, subord. nov. and Discocotylinea Bychowsky, subord. nov.

As a whole the order corresponds to the superfamily Dicliphoroidea of Price (=Dactylocotyloidea Brinkmann); however, it is not possible to utilize the present name (Price's name, nobis) because the family Diclidophoridea is aberrant in a number of connections and it would be incorrect to attribute type significance to it. p. 417

The division of the order into 2 suborders is based on a principal distinction in the method of forming the supporting skeleton of the clamps, to which we attribute a leading significance in the evolution of the present group of Oligonchoinea (see also Sproston, 1945b). It is quite probable that during subsequent studies it will be necessary to introduce an even larger number of basic subdivisions, but within the limits of both principal lines of development.

1. Suborder Mazocraeinea Bychowsky subord. nov.

Mazocraeidea, of middle and large sizes. The attaching armature of the adult individual consists of 4 pairs of clamps, one pair of edge hooks (always?) and 2 pairs of middle hooks. The clamps usually are of the same size, all with a complete chitinous capsule consisting of a number of separate parts or of a different size and a more or less reduced capsule. As an exception the number of clamps can be less than 8. The intestinal tract either has 2 clearly expressed trunks merging at the end and producing numerous lateral and internal outgrowths or it forms a net-shaped interlacing almost without traces of basic trunks.

Parasites of marine and transitory (anadromous or catadromous species, nobis) fishes--Clupeiformes and Perciformes, on the latter they are known basically from Scombroidei.

This suborder consists of two families--Mazocraeidae Price and Hexostomatidae Price.

1. Family Mazocraeidae Price, 1936

(Figs. 24, 25, 32, D, G. 41, 84, 113, B, 123, 124, 222-225, 263, 297, 298)

Mazocraeinea having middle and large sizes. The attaching apparatus consists of a disc weakly delimited from the body, bearing, among the adult forms, one pair of edge hooks, 2 pairs of middle hooks and 8 chitinous attaching clamps lying in 2 parallel rows along the lateral edges of the disc. As an exception the disc can be asymmetrical and bear a smaller number of clamps. The latter have a characteristic structure, they possess a complex chitinous capsule consisting of 5 separate parts connected with each other in a movable fashion. The anterior end has weakly developed cephalic glands. The eyes are absent among adult animals. The buccal cavity has 2 more or less large suckers. The intestinal tract is two-branched; its branches terminate blindly in the attaching disc or somewhat above it and form numerous lateral and interior outgrowths along their extensions. The male sex aperture and the uterus open along the medial side of the body by a common small atrium. The copulatory organ is armed with 2 types of hooks. The testes are numerous or there is only one. The ovary is flask-shaped, strongly elongated, and U-shaped. The vaginal ducts are paired or are absent.

Parasites of marine and transitory fishes--Clupeidae and Scombridae.

Type genus, *Mazocraes* Hermann, 1782.

In addition to the type genus, four more genera enter into the composition of the family: *Octostoma* Kuhn, 1829; *Mazocraeoides* Price, 1936; *Neomazocraes* Price, 1943; and *Pseudoanthocotyle* Bychowsky and p. 418
Nagibina, 1954; and possibly the fifth, *Grubea* Diesing, 1858.[1]

For this family, which was quite correctly isolated by Price (Price, 1936) from the formerly accepted diffuse family of Octocotylidae Beneden and Hesse, 1863[2], in the first place the structure of the attaching expressed in the fact that Price not only changed the name but showed more or less correctly its scope, which sharply differs from that of Octocotylidae in the understanding of Monticelli, (Monticelli, 1903).

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[1] The genus *Ophicotyle*--*gen. inq.* mentioned in the preceding text (see page 250) is also ascribed to this family; however, we do not consider it possible to include it in the genera of Mazocraeidae even with a question mark.

[2] Into the "family" Octocotylidae enter genera pertaining to Mazocraeidae, and also by present notions to other subsequent families which have 8 clamps. To say that Price simply changed the name of this family, as is done by Sproston (Sproston, 1946), would not be quite correct, although if the type genus retains its old name, *Octocotyle*, the family of Mazocraeidae should be called accordingly, according to the rules of nomenclature. The incorrectness of the indication of Sproston is

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clamps in the adult (Fig. 297) is characteristic. The latter were described sufficiently in detail in our common work with L. F. Nagibina (Bychowsky and Nagibina, 1954). Basically one must say that in spite of the considerable difficulties in the examinations of clamps in this group, which are further complicated by the different condition of the clamp in preparations and by different correlations of the separate parts depending upon the degree of opening for all genera, the presence of 5 mutually articulated parts forming a one-piece capsule, which opens only from one side, representing the opening of the clamp by means of the edges of which the pinching of the tissues of the gills of the host takes place, appears as characteristic for the family.

This capsule as a whole apparently corresponds to a much thickened and developed subcuticular membrane of other Oligonchoinea; however, it is not possible to say this with full certainty because the development of clamps of this type has not been studied. Likewise it is not possible to state whether altered edge hooks, in the places of which the clamps are incepted enter into its composition. As regards the separate parts of the clamp of Mazocraeidae, they are always strictly determined although they have different sizes and shapes among separate species and genera. Two plates form the basis of the clamps. The first (Fig. 297, A) has strongly serrated edges and is characterized by the presence of two rows of openings at its central part, apparently serving for the passage of several clusters of musculature. The second plate (Fig. 297, B) is more rounded, it adjoins the first or is partially superimposed upon it, at the same time the first one forms the lower part of the anterior valve and the second, the corresponding (part, nobis) of the posterior. The edges in the upper parts of the valves form two wide "lips" (Fig. 297, C, D), of which the first has larger dimensions and its ends are bent inside the clamps serving as its "springs." Apparently the last, the fifth part (Fig. 297, E) which has a horse-shoe shape fulfills the same functions. It is located in the posterior valve of the clamp. It is tempting to homologize the anterior "lip" of the clamp of Mazocraeidae with the parentheses of Chimaericolidae, both merging with each other at the anterior ends of the edge; however, it is possible that here occurs only a superficial similarity because of the identical function of both formations. The separate parts which were described are connected with each other in such a way that they practically form a single system devoid of large transparent areas and having a cup-shaped form. The opening of this cup is elongated in the transversal direction and its opening can be very large, although basically we almost never observe it as full. p. 419
As a rule the motion of both "lips" takes place within an angle of not more than 60 to 70 degrees. The described structure of the clamps is encountered

only within the limits of the family which is under study, and thus appears as their most important characteristic as has been indicated before. The second important characteristic of the family which is under study, strange as it may be, is a special type of armature of the copulatory organ. Generally speaking this can hardly be considered as an important character for the highest Monogenoidea because we know that the armature of the copulatory organ and of the sex atrium as a whole varies a great deal; however, in Mazocraeidae we observe a surprising constancy in this connection. In all the genera, the copulatory organ is armed with two large sickle-shaped thorns lying anteriorly along the sides of the sex cone (it is possible in the walls of the sex atrium) and usually within a row of much smaller little thorns lying somewhat posteriorly as is seen in the corresponding drawings (see Fig. 298). The exception is formed by Grubea in which the copulatory organ is represented, judging by the drawing of Palombi (Palombi, 1949), as a little corona of single hooks. Generally the status of this group in the system is not clear to us. We don't have our own material and the attribution of this genus is made conditionally, following Sproston (Sproston, 1946). If the data of Palombi are correct, and we have no basis to doubt it in this case, it is most probable that the genus Grubea should be removed from the composition of the present family. We do not do this only because we do not want to make a change which is not very convincing in this connection without any special research.

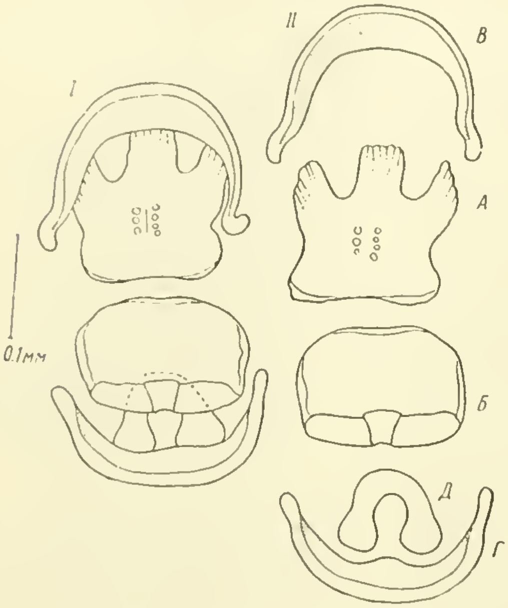

Fig. 297. Mazocraes alosae Hermann, structure of the attaching clamp. I--Chitinous parts of the capsule of the attaching clamp separatedand slightly compressed; on the top the anterior "valve" and on the bottom the posterior; II--Separate chitinous parts of capsule of the attaching clamp, explanation in text.

The genera Mazocraes and Octostoma are very close to each other and differ almost exclusively by the fact that in the first there are vaginal ducts, whereas in the second there are none all the remaining characters are completely secondary, in connection with which it is not fortuitously that Palombi and certain other authors united these genera. The genus Neomazocraes in its turn is very close to Mazocraes with which it is united by the presence of vaginal ducts and the nature of the posterior end of the body. The differences of both genera consist mainly in the somewhat different structure of the chitinous capsule of the clamps. Undoubtedly, Pseudoanthocotyle reaches the highest specialization for which the presence of considerable differences between the sizes of the 4th and the first 3 pairs of clamps is characteristic. At the same p. 420 time, the absence of vaginal ducts in this species is apparently a secondary phenomenon, just as in Octostoma.

The genus Mazocraeoides deserves attention. At first glance it seems the most primitive of the entire family. The presence of one testis, which is a primitive sign is characteristic for this genus. However, the structure of the attaching apparatus clearly bears the traits of secondary changes. Thus, the attaching clamps of these worms are located, not on the attaching disc but lie along the edges of the body, extending even into the first half of the body. Taking into consideration the fact that the clamps of Mazocraeidae are incepted at the places of the 2nd - 5th pairs of edge hooks it is possible to think that in the present genus we first encounter the displacement of edge hooks from the disc to the body of the animal in the post-embryonic period, or with the development of sex glands and other internal organs inside of a strongly growing attaching disc with simultaneous weak development of the body proper of the larva. One must suppose that the first variation is less likely; however, they both indicate secondary changes in the structure in comparison with Mazocraes and other "normal" genera. Undoubtedly secondary is also the structure of the copulatory organ in which there are special chitinous plates in place of the small hooks lying in the perpendicular plane in relation to the plane of the location of both large hooks. One must think that the presence of a single aperture for the vaginal ducts opening along the medial line of the dorsal side is also a secondary phenomenon. Thus, in spite of the seeming primitiveness, the Mazocraeoides are undoubtedly of a later origin than the remaining genera of the families.

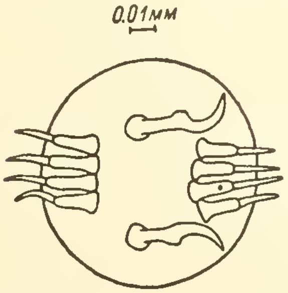

Fig. 298. Mazocraes alosae Hermann, copulatory organ of an adult worm from the gills of Alosa caspia (Eichw.), from the Delta of the Volga.

In conclusion, one cannot fail to note that within the limits of the family we see the evolution of the strengthening of the attaching contrivances of the worms in two directions. One direction where this strengthening takes place by means of strong development of the fourth pair of clamps is characteristic for Pseudoanthocotyle. Another method we see in Mazocraeoides where strong attachment is attained by means of the dispersement of the attaching organs along a larger portion of the length of the body. The last direction, as will be seen from what follows, is apparently more progressive and is encountered in a number of highly organized forms.

2. Family Hexostomatidae Price, 1936

(Figs. 37, 299)

Plagiopeltinae Monticelli, 1903.

Mazocraeinea, having large sizes in the adult state. The attaching apparatus consists of a widened disc, weakly delimited from the body on which are located 2 pairs of middle hooks and 8 clamps, secondarily changed into suckers. The clamps lie in two symmetrical groups but form almost one straight (group, nobis) so that the first pair (according by the time of inception), which usually has smaller dimensions, is located near the medial line of the disc and the subsequent ones toward its periphery to the right and to the left. The clamps are equipped with 3 chitinous parts p. 421 representing the remnants of the reduced capsule, apparently of the mazocraeid-type. The anterior part of the body bears a buccal opening lying terminally. The eyes are absent. The buccal cavity has 2 suckers. The intestine is powerfully developed and forms a net-like interlacing of the branches which begins immediately behind the esophagus and terminates in the attaching disc. The basic trunks of the intestines are noticeable only at the very beginning of their extensions. The male copulatory organ is not armed but opens outside together with the opening of the sac-shaped uterus. The testes are numerous. The ovary is of the flask-shaped type but has a large number of curvatures and outgrowths and forms a compact mass, mainly U-shaped with the apex turned toward the anterior end of the body. The vaginal ducts are double and merge anteriorly into one which opens outside dorsally. The end of the unpaired vaginal duct is armed with 2 large chitinous plates with an indented interior edge.

Parasites of tunas and of the families close to them (Cybiidae and Carangidae).

Type and only genus, Hexostoma Rafinesque, 1815.

Price correctly elevates the subfamily Plagiopeltinae earlier (Plagiopeltis Diesing =Hexostoma Rafinesque) abstracted by Monticelli (Monticelli, 1903) into the rank of a family because there is no doubt that it is a very individualized group which cannot be included into any of the known families of Oligonchoinea.

The general plan of the structure of Hexostomatidae principally does not differ from the one of other Oligonchoinea, but it has a number of very interesting peculiarities in the structure of the attaching apparatus

and chiefly in the clamps. A typical clamp of *Hexostoma*[1] has the shape of an oval sucker stretched longitudinally in reference to the body but in transverse direction of the clamp (Fig. 299). Thus the half of each clamp lying toward the middle axis of the body of the worm corresponds to the anterior valve of typical clamp of Oligonchoinea and the opposite one--to the posterior one. The "clamp" of *Hexostoma* (Fig. 299, A) represents a sucker which has a weak cup-shaped form which acts, in contrast to all remaining Oligonchoinea, precisely as a sucker. One should only take into consideration the secondary nature of this "sucker" which is substantiated by its morphology. It is flatter than the usual sucker and it is divided into 2 depressions right and left in connection with the presence of a more or less strong thickening of the middle chitinous piece along the middle line. Although the latter is usually described as having an irregular form [see the description and drawings of Goto (Goto, 1894)], actually it represents, judging by our preparations, a fully symmetrical formation with insignificant differences in the details of right and left sides. The middle piece (Fig. 299, B) lies with its long axis along the longitudinal axis of the clamp so that its anterior half is located in the anterior part of the clamp and the posterior--in the posterior and hence in the shape of a flat, cake-shaped plate folded in half longitudinally and thus are formed the right and left wings. The rib of the plate faces edgewise toward the ventral side with both free edges toward the dorsal. The rib is somewhat thickened and compressed in the anteroposterior direction, in connection with which during observation of preparations it gives the impression of an x-shaped figure which is described by a number of authors (Price, 1943; Sproston 1946, and others). Actually, as is clear from what has been said, this is p. 422
a purely optical phenomenon. The right and left wings are of ear-shaped form with more or less even edges. The middle part of each wing is pierced by 3-4 openings of irregular form analogous to the ones of the bottom of the plate of the clamp of Mazocraeidae. Apparently because of the necessity of the attachment of the plate from the ventral side it forms thickening in the central part which unites both wings and has one large opening in the center. This opening serves, as we succeeded in observing during microdissection for the attachment of the powerful structures of the musculature. It seems to us that the middle piece of the clamp represents the remaining part of the capsule of the clamp of Mazocraeidae and most probably basically the plate which forms the bottom. This is even more likely since the locations of both formations fully correspond to each other. As regards both edge plates of the clamp of *Hexostoma* (Fig. 299, C and D), they have a fully determined but not symmetrical form. At the same time, asymmetry is both longitudinal and

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[1] In addition to the literary data we have utilized our own relatively sparse materials on *Hexostoma grossum* Goto, 1894.

transversal. However, one must pay attention to the fact that a large part of each plate is located in the anterior half of the clamp. In this connection it is possible that these are the remnants of the anterior "lip" of Mazocraeidae; however, the certainty of this is very doubtful. As regards our supposition

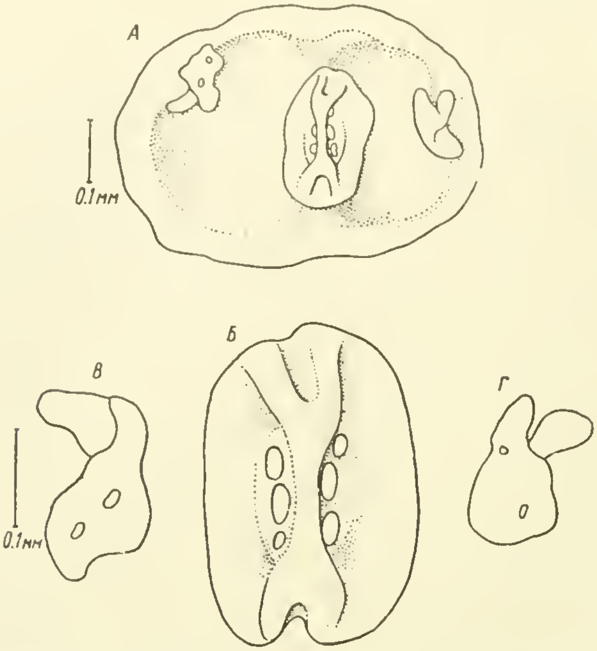

Fig. 299. *Hexostoma grossum* (Goto), attaching clamps and its chitinous parts. Explanation in the text.

about the homology of the clamps of Hexostomatidae with the parts of the capsule of Mazocraeidae, it is also substantiated by the plate-like make-up of these formations. As a matter of fact, as is self-evident, special studies on live subjects and particularly the study of early postembryonic stages are indispensable for any final confirmations, whatever they may be.

As regards the internal organization of Hexostomatidae, the greatest interest is aroused by the structure of the intestines, which obviously acquired a most complex net-like structure secondarily. Only in *Microcotyle reticulata* Goto apparently is there an analogous structure. However, in this species one can also notice the basic trunks of the intestine throughout a rather long extension. p. 423

The sex system of Hexostomatidae resembles the one of Mazocraeidae as well as the one of Microcotylidae to an equal degree, and its sharp asymmetry in the location of the beginning of both vitelline ducts and correspondingly of the place of departure of the vaginal trunks can be considered as its only important difference.

As a whole Hexastomatidae undoubtedly are secondarily changed species, and it is most probable that they are close to Mazocraeidae. This is indirectly substantiated also by the parasitizing of fishes which are close phylogenetically as well as ecologically.

2. Suborder Discocotylinea Bychowsky, subord. nov.

Mazocraeidea, of middle and large sizes. The attaching armature of adult individuals consists of 4 or more pairs of clamps and one pair of edge and 1-2 pairs of middle hooks. In a number of cases the hooks can be fully or partially absent. The clamps have a chitinous supporting apparatus, but the latter never forms a capsule, but consists of separate little parts articulating at their ends. The intestine is with 2 trunks and as an exception is net-shaped.

Parasites of marine and fresh water fishes, basically Perciformes and Clupeiformes.

The suborder consists of 7 families: Discocotylidae Price, Anthocotylidae Bychowsky, fam. nov.; Plectanocotylidae Bychowsky, fam. nov.; Diclidophoridae Fuhrmann; Microcotylidae Taschenberg; Protomicrocotylidae Poche; Gastrocotylidae Price.

The system of the present suborder has not yet been completely analyzed. It is possible to suppose that its juxtaposition to Mazocraeinae is in order and will hardly ever be subjected to doubt. As regards the scope of Discocotylinea, it is possible that in the future this suborder will have to be subdivided by extracting Plectanocotylidae and the related Gastrocotylidae from it.

1. Family Discocotylidae Price, 1936

Octocotylidae auct. part.

Discocotylinea, having middle sizes. The attaching apparatus consists of a disc more or less well-delimited from the body, which carries one pair of middle hooks and 4 pairs of attaching clamps in the adult forms. Each clamp is equipped with 5 chitinous plates. The eyes are absent among adult forms (the larvae have 2 eyes or one double). The intestines are double or in the shape of a single trunk forming a number of outgrowths. The copulatory organ has a chitinous armature in the shape of a small pipe. It is either not armed or is completely absent. The testes are numerous or there is only one of them. The vaginal ducts are either present or absent. The animals are single or growing in pairs. The other characteristics are similar to those of Mazocraeidae.

Parasites of migratory and fresh water fishes (Salmonidae, Thymallidae, Cyprinidae, Catostomidae and Cobitidae.

The family is divided into Discocotylinae Price, and Diplozooninae Palombi.

The present family, in the scope accepted by us, comprises only part of the species ascribed to it by Price (Price, 1936) and Sproston (Sproston, 1946) and parasitizes practically only fresh water fishes.

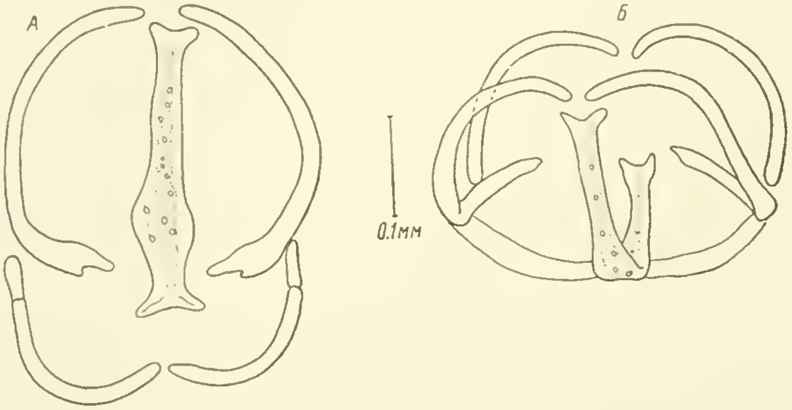

Fig. 300. Discocotyle sagittata (Leuckart), chitinous parts of the attaching clamp. A--An artificially unfolded view; B--In normal condition.

In addition to the structure of the adult animals, the presence of larvae which possess still another pair of fully developed clamps capable of immediate attachment in addition to the hooked, partially reduced (Diplozoon) armature is characteristic for these species. This peculiarity among forms bearing 4 pairs of clamps in the adult state is encountered only among representatives of the present family and generally--only on the highly specialized Microcotylidae. Also important is the circumstance that in the larva of Discocotylidae there is one pair of middle hooks which remains without changes in the adults, in contrast to the majority of 8-clamped forms among which one or more pairs of middle hooks appear, as a rule, either during the embryonic or postembryonic period. Similar relations are observed among Mazocraeidae, Plectanocotylidae, Anthocotylidae, Hexostomatidae and even among such a remote family from the families enumerated as Chimaericolidae. Only Diclidophoridae have one pair of middle hooks in the adult state just as the Discocotylidae (certain Diclidophoridae apparently loose their middle hooks in the postembryonic period--see page 431), but their larvae are easily distinguished by the absence of the clamps, whereas the adults--by a number of anatamo-morphological characteristics (see pages 431 - 438).

What has been indicated seems to us fully sufficient to consider the separation of the given group into a special family as correct or in order. Its isolation undoubtedly is linked in the historical aspect with a change from parasitizing marine fishes to living on fresh water fishes.

The attaching clamps of Discocotylidae (Fig. 300) are arranged somewhat simpler than among the preceding families of this order. They have muscular walls in which 5 chitinous plates (sclerites of other workers, nobis) are located. The first of them lies in the medial line across both valves in such a fashion that its larger part is located in the anterior valve. This plate corresponds and is homologous to the basal plate of Plectanocotylidae (see page 429) and usually has ends which are of characteristic shape for separate species, to which the corresponding muscular clusters are attached. Along the lateral edges of the anterior valve lie the 2 plates, which are mirrored in relation to each other, with their anterior ends drawn close to each other and to the anterior end of the middle plate. The posterior parts of these plates extend beyond the limits of the anterior ones and are located in the posterior valves in such a fashion that their ends are oriented toward the posterior end of the middle plate. On the whole, there are the three elements which form the spring system of the clamp. At the place of the transition of the lateral plates into the posterior valve, to each of which is articulated a frail plate which proceeds along the edge of the posterior valve toward the middle where they very often adjoin very closely against each other. Frequently these plates are connected together by a special tendon (compare with the posterior "lip" of Plectanocotyle!--page 429). As a whole, the clamps of Discocotylidae have, as is apparent from the description, mirrored right and left halves and a different structure of the anterior and posterior valves. With this, one must bear in mind that the posterior valve is less mobile than the anterior, which is connected with the nature of its location in relation to the body of the animal. It is connected to it by its large surface, whereas the anterior valve is more free. Let us note also that we can speak with a high degree of probability about the homology of the lateral plates of the anterior valve with the parentheses of Chimaericolidae and the corresponding plates of Plectanocotylidae, whereas the plates of the posterior valve can be subjected to homologization only with great difficulty. However, as will be seen from that which follows (see page 429), they are most probably homologous to the lip and the lateral plates of the posterior valve of the clamp of Plectanocotylidae and also to the lip of the posterior valve of Mazocraeidae. p. 425

1. Subfamily Discocotylinae Price, 1936

(Figs. 228-230, 300)

Single Discocotylidae with two-branched intestines. There is a copulatory organ. The testes are numerous or in the shape of a single, large, follicular mass. The vaginal ducts exist or are absent.

Parasites of Salmonidae, Thymallidae, Catostomidae and Cyprinidae.

Type genus, *Discocotyle* Diesing 1850.

In addition to the type genus another genus, *Octomacrum* Mueller, 1934, also belongs here.

Both genera differ from each other by the presence (*Discocotyle*) or absence (*Octomacrum*) of vaginal ducts and by the armature of the copulatory organ.

It is most probable that the changes in the structure of *Octomacrum* are secondary in relation to *Discocotyle* which is more ancient in origin. This is indirectly confirmed by the fact that the latter genus is encountered both on transitory (migratory, *nobis*) and freshwater fishes, whereas the first is only on fresh water fishes.

2. Subfamily Diplozooninae Palombi, 1949 p. 426

(Figs. 32, F, 113, F, 122, 231-234)

Discocotylidae, grown together in pairs in the adult state. The intestine in all stages of development is in the shape of a pipe which has lateral outgrowths. The testis is single and rounded. The male sex ducts of one individual grow together with the corresponding female ducts of the other.

Parasites of Cyprinidae and Cobitidae.

Type and only genus, *Diplozoon* Nordmann, 1832.

Widely distributed in Palearctica. A genus which does not have many species. Its isolation by Palombi (Palombi, 1949) into an independent superfamily seems fully correct to us. The specialization of *Diplozoon* has gone very far. This is expressed not only by the singular growing together of the young individuals, without which single samples cannot continue further development, but also in the fact that the larva of these worms is deprived of the edge hooks and its attaching disc has only one pair of middle hooks and a pair of attaching clamps. In connection with the question concerning the formation of subsequent pairs of clamps, the absence of edge hooks is very interesting, which has already been mentioned (see page 101).

2. Family Anthocotylidae Bychowsky, *fam. nov.*

(Figs. 6, 42, 104, 301)

Discocotylidae Price, 1936, *part.*; Anthocotylinae Price, 1936.

Discocotylinea having middle and large sizes. The attaching apparatus consists of a disc more or less delimited from the body, bearing one pair of edge, 2 pairs of middle hooks and 4 pairs of attaching clamps of the discocotylid-type but having 1-3 more supplementary chitinous plates in addition to the 5 basic ones. The hooks are located on an elongated finger-shaped or linguaform outgrowth of the lower part of the disc. The eyes are absent among the adult forms. The copulatory organ has chitinous armature in the shape of a little corona of hooks, more seldom the armature is absent. Vaginal ducts exist. They open ventrally by the lateral apertures or, as an exception, the vaginal ducts are absent (*Vallisia*). The remaining characteristics are similar to the ones of Mazocraeidae.

Parasites of marine fishes (Gadidae, Bramidae, Carangidae, and Gempylidae).

Type genus, *Anthocotyle* Beneden and Hesse, 1863.

In addition to the type genus the genus, *Winkenthughesia* Price, 1943, and probably *Vallisia* Parona and Perugia, 1890, enter into the composition of the family.

As was already indicated in the description of Discocotylidae, the presence of 3 pairs of chitinous hooks on the attaching disc of the adult animals is a characteristic distinction of the present isolated family, in contrast to one pair in Discocotylidae. However, in addition to this, although the clamps of Anthocotylidae are built along the type common to Discocotylidae they, nevertheless, differ by the presence of supplementary plates. Thus, a small unpaired plate which adjoins by its anterior end the posterior end of the large (basic) unpaired plate and with its posterior articulating with both lateral plates of the edge of the posterior lobe appears in the posterior valve behind the middle plate of *Anthocotyle* (Fig. 42). In *Winkenthughesia* (Fig. 301) there is no similar formation but there are 2 p. 427
symmetrical plates located anteriorly from both lateral plates of the posterior lobe of the clamp. There is something similar in *Vallisia* in which, judging by the drawing of Monticelli (Monticelli, 1912--we did not possess our own material), there are 2 pairs of plates lying parallel to each other in the posterior lobe instead of one pair.

As regards the separate genera, one must consider *Winkenthughesia* as the most "normal." To this genus is also related a species described as *Octostoma* (=*Kuhnia*) *bramae* (Parona and Perugia, 1896) about which we have already spoken (see page 259). In 1955 we received a small amount of material of this species from Brama raii (L.) from Naples and on the basis of this we succeeded in establishing that it is very close to the type species of Winkenthughesia--W. thyrsites (Hughes) a species which should consequently be named Winkenthughesia bramae (Parona and Perugia, 1899) Bychowsky, comb. nov. The type of the family, Anthocotyle, is undoubtedly a secondarily changed genus because the enlargement of the fourth pair of clamps, as we have shown with L. F. Nagibina (1954), is a new formation which has an adaptive significance. The status of the genus Vallisia (Fig. 6) in the family is uncertain. Judging by the description of Monticelli (Monticelli, 1912), this genus differs from the two preceding ones not only by a peculiar asymmetry of the body but also by a number of important peculiarities of internal organization. Thus, according to Monticelli the copulatory organ of Vallisia is deprived of armature and the vaginal ducts are also absent. Thus, if one should consider these data as authentic, Vallisia strongly differs from the two preceding genera and the simplification of its organization is indisputably secondary. However, we have certain doubts about the data of Monticelli. Thus, his description and representation of the posterior end of the disc forces us to suppose that he did not notice 2 pairs of hooks besides the ones he has shown because the pair which was indicated by him is undoubtedly the second (large) one of the middle hooks. p. 428 In the description of the sex system he does not indicate the presence of the canalis genito-intestinalis which cannot be absent in this genus. In this connection, the data of Monticelli concerning the absence of vaginal ducts arouses doubt. The terminal openings of the excretory system expressed by him on the drawings of the sections (Table 2, G), hardly represent such--more likely these are sections through the terminal part of the vaginal ducts and consequently the excretory "ampules" expressed in the same plate in drawing 10 can

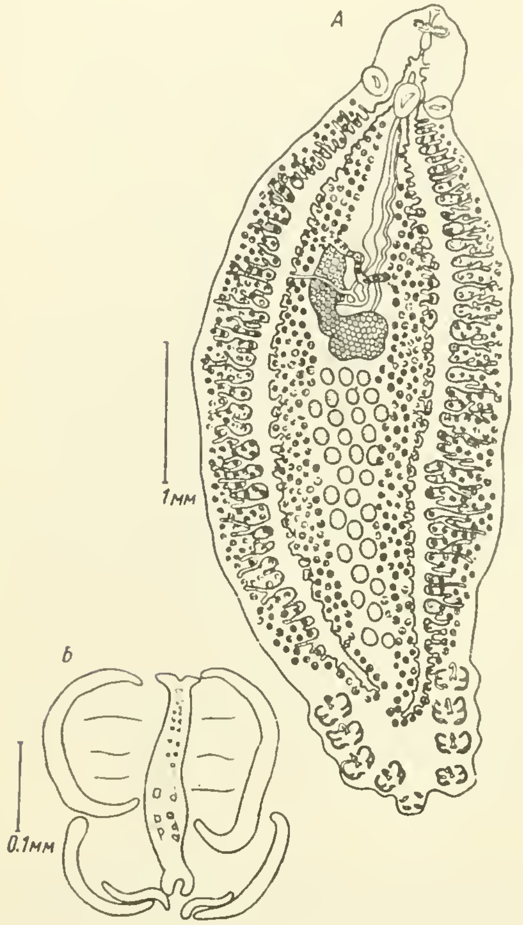

Fig. 301. Winkenthughesia bramae (Parona and Perugia). A--Adult worm from the gills of Brama raii Bl. Sch. from the Bay of Naples (Mediterranean Sea); B--Artifically unfolded clamp.

hardly be accurate. It is understandable that this can be verified only in the actual material, but if it be so then Vallisia should be ascribed to the present family, but for the time being the doubt of the veracity of its belonging in Anthocotylidae remains. Price (Price, 1943b) separates Vallisia into a subfamily on the basis of its asymmetry, the presence of the testes in front of the ovary, the number and the shape of the hooks of the attaching disc. The considerations of Price are important; however, we do not consider it possible to accept his opinion without the verification of the actual material and we think it more justified to leave open the question about the systematic separation of Vallisia.

3. Family Plectanocotylidae Poche, 1925

(Figs. 88, 302)

Plectanocotylinae Monticelli, 1903; Mazocraeidae auct.

Discocotylinea, having middle sizes. The attaching apparatus consists of a disc weakly delimited from the body, bearing, among adult forms, one pair of edge, 2 pairs of middle hooks, and 6-8 attaching clamps. The hook armature is located on the posterior end of the disc transformed into a more or less long linguaform outgrowth. The clamps possess a complex chitinous capsule consisting of 6-7 basic parts connected with each other in movable fashion. The eyes are absent (the larvae probably have one double eye). The copulatory organ has chitinous armature in the shape of a long cluster of needles. The testes are numerous and are situated either only behind the ovary or also in front of it. The vaginal ducts are absent. The other characteristics are similar to the ones of Mazocraeidae.

Parasites of marine Perciformes (Triglidae, Serranidae, Carangidae, Trichiuridae).

Type genus, Plectanocotyle Diesing, 1850.

In addition to the type genus, Octoplectanocotyle Yamaguti, 1937 and Vallisiopsis Subhapradha, 1951 are also ascribed here.

Monticelli (Monticelli, 1903) first established the special subfamily Plectanocotylinae into which he included 2 genera, Plectanocotyle Diesing and Phyllocotyle Beneden and Hesse, the latter genus was later made synonymous with the first. This subfamily was ascribed by Monticelli to the family Hexacotylidae, also established by him. Inasmuch as Hexacotyle (=Diplobothrium in the same work of Monticelli, =Hexostoma according to contemporary nomenclature) clearly has nothing in common with Plectanocotyle, Poche (Poche, 1925) established a new family Plectanocotylidae indicating

that 3 genera are related to it (it is not clear to us which third genus Poche had in mind because in the text of his work the names of the genera are not cited). In his doctoral dissertation Price (Price, 1936) ascribed the genera *Phyllocotyle* and *Plectanocotyle* to the family Mazocraeidae without indicating his reasons for doing so. Sproston (Sproston, 1946) in her résumé does not agree with Poche or with Price and retains p. 429
the subfamily Plectanocotylinae Monticelli ascribing it to the family Discocotylidae Price.

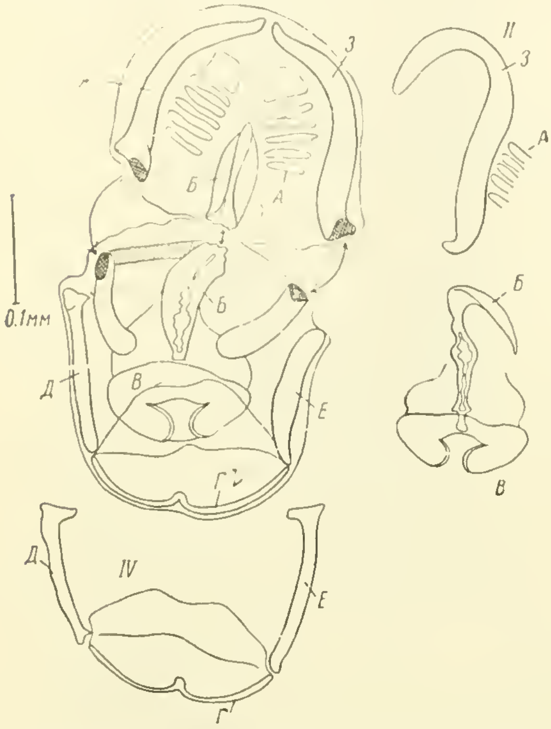

Fig. 302. *Plectanocotyle gurnardi* Beneden and Hesse, attaching clamp of adult worm from the gills of *Trigla gurnardus* L. from the region of north west Ireland (Atlantic Ocean). I--Attaching clamp cut in half and unfolded; on the top--anterior valve and on the bottom the posterior; II, III, IV--Separated (steamed apart or dissected, *nobis*) chitinous parts of the clamp. Explanation in the text.

We had at our disposal considerable material of *Plectanocotyle* from the Mediterranean Sea and a number of regions of the North Atlantic and several samples of *Octoplectanocotyle* from the Mediterranean Sea.[1]

On the basis of the study of this material we succeeded in obtaining a number of new data about the structure of Plectanocotylidae, and first of all of their attaching apparatus. The clamps of *Plectanocotyle* (Fig. 302) resemble those of Mazocraeidae but differ slightly by the fact that their anterior valve does not have a continuous chitinous surface but basically consists of muscular and connective tissue parts similar to the valves of Discocotylidae (see page 425). In contrast to the anterior valve, the posterior one represents a similar strong chitinous formation as in Mazocraeidae. As a whole, the clamp bears 7 separate chitinous parts. On its bottom is located a flexible plate, not very wide in the anterior part and bearing wing-shaped outgrowths in the posterior part (Fig. 302, B). This plate corresponds to the central plate (which bears the aperture) of Mazocraeidae and apparently is homologous to it. It lies in such a way that its smaller anterior part is located in the anterior valve. The plate articulates by its posterior part to the second plate which has the shape of a transversly elongated oval, and with a deep festoon-shaped thickening on the posterior edge (Fig. 302, C). This plate corresponds and is homologous to the second plate of the bottom of the clamp of Mazocraeidae and fulfills the same function. Immediately posterior to the plates just described a third one is located (Fig. 302, D) which forms a "lip" of the posterior valve in the shape of a very thin singularly shaped petal with a thickened posterior (exterior) edge. Attention is attracted by the fact that p. 430 this thickened edge has a characteristic depression in the middle bisecting, so to speak, the edge of the plate into two parts, which possibly indicates the origin of this unpaired formation at the expense of two earlier existing elements (see page 425).

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[1] The representatives of the genus *Octoplectanocotyle* were first encountered in Europe by us.

Two lateral, plank-shaped separatenesses (Bychowsky calls all the sclerites separatenesses or plates, *nobis*) are located along the edges of both connecting plates in the posterior valve (Fig. 302, G, H) articulating with 2 curved parentheses which lie partially in the anterior valve of the clamp along its edges and partially externally into the posterior valve and form springs similar to the ones of Chimaericolidae and Diclidophoridae, and are undoubtedly homologous to them. At the same time one can suppose that these two planks "parentheses" are also homologous to the anterior unpaired lip of Mazocraeidae; however, this could be erroneous (see page 425). Small chitinous bands or strips, the number of which varies from 5 on each side to 8-9, lie symmetrically and parallel to each other between the lateral parentheses in the middle plate in *Plectanocotyle* (Fig. 302, A). In isolated cases, these strips can partially merge with each other and form more or less large membrane-shaped plates which line the anterior surface of the valve. In *Octoplectanocotyle* the clamps are arranged in a manner similar to what has been described, but they differ by the absence of strips of the anterior valve. On the whole, speaking about clamps in Plectanocotylidae we can conclude that they are arranged more simply than the ones of Mazocraeidae and apparently are phylogenetically closer to the initial ancestral forms.

As is seen from the description of the clamps of Plectanocotylidae, they sharply differ from the "discocotylid-type" (see page 425) and consequently one cannot in any way agree with Sproston (Sproston, 1946) regarding the systematic status of the group under examination. On the other hand, the unification of *Plectanocotyle* with *Mazocraeidae* into one family also does not seem correct to us because the differences in the structure of the clamps in both groups are sufficiently important, and besides that there are other important characters and signs such as the structure of the copulatory organ and especially the presence, in Plectanocotylidae, of special outgrowths of the posterior edge of the disc, bearing chitinous hooks; whereas in Mazocraeidae they lie on the posterior undifferentiated end of the disc.

The correlation of genera is obvious. Thus, without any doubt Octoplenocotyle is a more primitive genus than Plectanocotyle. The last genus is very interesting in the fact that it bears only 3 pairs of clamps on the attaching disc, i.e., it ceases development at an earlier stage than all other closely related groups. The fact that this is so and that this is not a secondary reduction as in Diclybothriidae is indicated by the absence of traces of the inception of the fourth pair of clamps. It is possible that during careful study of live subjects it will be possible to show that an additional pair of edge hooks, besides those on the outgrowths are preserved on Plectanocotyle. By its location it will be possible to say definitely which of the pairs of clamps does not develop. As is understandable, it is most probable that it is the fourth pair.

Vallisiopsis undoubtedly is a secondarily changed genus for it has considerable asymmetry in the structure of the body. It is noteworthy that Chauhan [Chauhan, 1900, (sic date)] refers this genus to Gastrocotylinae, i.e., likens them with the last Plectanocotylidae, This, as will be seen later, is fully justifiable (see page 468).

4. Family Diclidophoridae Fuhrmann, 1928 p. 431

(Figs. 54, 86, 87, 101, A, 226, 227, 303-307)

Choricotylidae Rees and Llewellyn, 1941.

Discocotylinea having small, middle, and large sizes. The attaching apparatus has 8 chitinous attaching clamps, one pair of edge hooks and one pair of middle hooks. In a number of species the hook armature can be absent (?). The attaching clamps are arranged according to the "discocotylid-type", but their chitinous apparatus consists of 8 separate parts. Some of them can partially merge with each other forming complexly arranged plates in this manner. For the majority of the genera the asymmetry of the right and left halves of the clamps as a result of the uneven development of the paired chitinous plates is characteristic. Among the adults and apparently among the larvae the eyes are completely absent. The copulatory organ is usually armed with a corona of chitinous hooks. The vaginal ducts are absent for the most part; if they exist they are double or more rarely single. The remaining characteristics are similar to those of Mazocraeidae.

Parasites of marine fishes, Gadiformes (Gadidae), Macuriformes (Macruridae), Perciformes (a number of families) and Pleuronectiformes (Bothidae and Pleuronectidae) and Tetrodontiformes (Tetrodontidae). They are also encountered on parasitic isopods.

Type genus, Diclidophora Diesing, 1850.

In addition to the type genus into the composition of the family enter Choricotyle Beneden and Hesse, 1863; Cyclobothrium Cerfontaine, 1895; Echinopelma Raecke, 1945; Diclidophoropsis Gallien, 1937; Heterobothrium Cerfontaine, 1895; Pedocotyle MacCallum, 1913.[1]

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[1] The genus "Cyclocotyla" apparently pertains to the present group, but we do not consider it possible to indicate it in the enumeration of the genera even with a question mark (see page 225).

The present family has a very confused synonymy both of genera as well as of separate species. It will be sufficient to indicate that some separate species have more than 10 synonyms. In the present work we cannot dwell on this but we shall only indicate that the nomenclature of the genera accepted by us is the same as the one in the résumé of Sproston (Sproston, 1946).

The family is usually divided into 2 subfamilies differing from each other by the nature of the action of the clamps. For one subfamily (Diclidophorinae Cerfontaine, 1895) it is accepted that the clamps of its representatives have a pinching action, i. e., act as real clamps; whereas for the other (Choricotylinae Sproston, 1946; =Cyclotylinae Price, 1943) that they function as suckers. Actually, this is the only concrete difference which is offered by the authors as the basis for the division of the family. Thus, Price (Price, 1943a) differentiates Diclidophorinae by the presence among them of the "clamp-shaped" suckers and Cyclocotylinae--by "cup-shaped" suckers. Sproston (Sproston, 1946) writes simply that in the first subfamily the organs of attachment act as clamps, whereas in the second--as suckers, mentioning at the same time that the musculature extending from the body into the clamps terminates in Choricotylinae by a special sucker on the interior side of the capsule of the clamp, whereas in Diclidophorinae it merely enters the clamp from its interior edge.

As the first source of these opinions can be considered the statement of Cerfontaine (Cerfontaine, 1895) who, describing the new species Diclidophora labracis (=Choricotyle labracis according to the present system), of which he found only one specimen, indicates that the p. 432 organs of attachment of this species act as suckers in the real sense of the word and especially considers the question about the peculiarities of the musculature and the chitinous elements of the "suckers." Nevertheless, the question about the attachment of Diclidophoridae is not so simple and can hardly be solved in the way it has been attempted. However, it is possible to suppose that a basic means of attachment for all Diclidophoridae is the pinching of the tissues of the host, i. e., the action of the attaching organs according to the principle of the clamp. With this it is impossible to deny also the fact that the elements of adhesion play an undeniable, although secondary role; in other words, we do not deny the action of the clamps also as suckers, but this refers to all Diclidophoridae as a whole and is not the basic function of the mechanism of attachment. The study of the actual material of genera--Diclidophora, Choricotyle, Diclidophoropsis and Heterobothrium serves as a basis for our point of view. One must add that the first 2 genera are the most numerous of all the 7 known.

However, before speaking about the nature of the attaching organs we should make a short survey of their structure among different genera. The study of separate parts of the clamps and other clamps as a whole was made on material fixed in the natural condition and not removed from the gills or other organs of the body of the host. This is very important to our subsequent considerations. The separate parts of the clamps were studied not only and not so much in whole mounts as by means of parts disarticulated from each other and from the musculature in glycerin or glycerin-gelatin with the preservation of their natural location and form. The clamps of the representatives of the genus Diclidophoropsis are the closest to the initial" discocotylid-type." In contrast to the indications of Brinkmann (Brinkmann, 1942) and Sproston (Sproston, 1946), who consider the asymmetry of chitinous elements of clamps and the mirror-like (bilaterally symmetrical, nobis) state of the latter on the right and left sides of the body as the basic characteristic peculiarity of Diclidophoridae which enables us to juxtapose it to the rest, in Diclidophoropsis the structure of the clamps (Fig. 303) is the same on both sides of the body and their chitinous elements have an almost symmetrically mirror structure of the right and left halves. This was first shown by Gallien (Gallien, 1937) who described the present genus and, as a matter of fact, it is also mentioned by Sproston (Sproston, 1946), in spite of the fact that this contradicts her own considerations. The clamp has two unequal plates (sclerites of other workers, nobis) lying along its middle line. The first (Fig. 303, A) the basic and largest, is more or less of the same width along its entire length and lies in such a fashion that its upper T-shaped, widened end comes close to the most exterior edge of the clamp corresponding to the edge of the anterior valve of the clamps of the usual construction. The lower end, also T-shaped and widened, lies approximately in the center of the clamp or somewhat closer to the posterior edge. From this end and articulating with it, the second smaller one extends posteriorly (Fig. 303, B) terminating near the posterior edge of the clamp (near the edge of the posterior "lip") in a small widening. The homology of these plates does not cause any doubt. The first is homologous to the basic plate of Discocotylidae and the second--to the corresponding plate in Anthocotyle. For the sake of convenience during further comparisons, we shall designate the first plate as basic middle and the second as the supplementary middle. The anterior end of the basic middle plate articulates with two "lateral anterior" plates (Fig. 303, C and D) which extend along the edges of the clamps approximately to its middle where they curve strongly and pass from the edge onto the sphere of the clamp and terminate, articulating p. 433

correspondingly from each side, with the T-shaped posterior end of the T-shaped posterior end of the basic middle plate. At the place of the sharp curvature of the lateral anterior plates they form a more or less clearly expressed little hump which serves for articulation with the "lateral middle" plates (Fig. 303, E and F). The latter, starting from the above-mentioned hump of the lateral anterior plates, extend along the edges of the clamp posteriorly and terminate approximately at the three-quarter level of the total circumference of the clamp. Somewhat lower and also along the edge begin the paired "posterior lateral" plates (Fig. 303, G and H) which terminate, articulating with the posterior end of the supplementary middle plate. As is seen from the description, the lateral anterior plates are equivalent to the lateral plates of the anterior valve of the clamps of Discocotylidae and are undoubtedly homologous to them. As regards the middle and posterior lateral plates, they correspond together to the lateral plates of the posterior valve of the clamp of Discocotylidae but it is not clear whether they are all homologous to these plates and, in other words, whether there is one lateral plate divided into two parts on each side, or whether here occurs a new formation of an extra pair of lateral plates.

Along with the above-mentioned 8 skeletal parts the posterior half of the clamp bears a number of cuticular thin sticks lying in parallel rows on the interior surface of the right and left quarters formed by the basic plates. The musculature of the clamps is rather powerful. The cluster of the muscles extending from the peduncle on which a clamp is located lies almost in the middle and terminates in the clamp, attaching itself to a special crest on the dorsal side of the anterior end of the basic middle plate. In the more open position the clamp nevertheless appears in the shape of an ordinary cup--its anterior part is always more or less curved toward the ventral side, as a result of which the basic middle plate resembles a constantly bent spring just as among the preceding families.

We observe further morphological changes in the structure of the clamps of the Diclidophoridae among the representatives of Choricotyle in which a different degree of asymmetry of separate elements with the retention of the same number of basic chitinous plates (Fig. 304) is observed. Thus, the basic middle plate has the upper and the lower T-shaped outgrowths with differently developed right and left halves. At the same time the lateral anterior plates also become different. One of them becomes considerably larger and of somewhat different shape than the other (Fig. 304, C and D) as a result of which the clamp acquires a rather marked asymmetry of the right and left halves. With this, in respect to the p. 434
longitudinal axis of the body of the animal, that side of the clamp which lies outwardly (that is to the right from the right side of the body, and the left from the left) has a large anterior lateral plate and perhaps both remaining ones. The muscular cluster extending into the clamps from the "peduncle" in connection with this is nevertheless also displaced and approaches from the ventral side which is more weakly developed. As a

rule the muscular cluster terminates by a special sucker near the internal section of the clamp. In spite of the indication (to the contrary, *nobis*) by the several authors, the clamp of *Choricotyle* in the normal state is not open "sucker-shaped" or "cup-shaped", but is typically clamp-shaped.

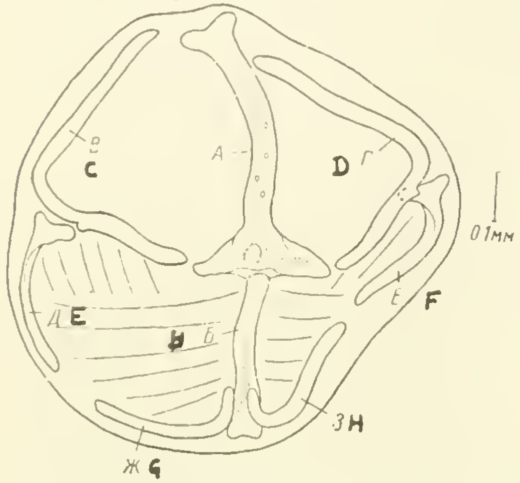

Fig. 303. *Diclidophoropsis tissieri* Gallien, unfolded clamp of an adult individual from the gills of *Malagocephalus laevis* (Lowe) near the western shores of England (Atlantic Ocean). Explanation in the text. (In this and subsequent drawings, 304-306, the homologous parts of the attaching clamp are indicated by the same letters.)

The clamps of *Heterobothrium affinis* (Linton, 1898) studied by us have a similar degree of complexity (Fig. 305). In contrast to *Choricotyle*, the upper end of the basic middle plate is weakly widened and is almost completely symmetrical, whereas the lower end is sharply asymmetrical with an outgrowth at one side. In addition to this, the middle part of this plate (Fig. 305, A) forms a large triangular membrane-shaped growth oriented in the same direction as the lower large outgrowth.[1]

The anterior lateral plates are approximately the same size, just as are the remaining lateral plates.[2] The muscular cluster forming the weakly developed sucker enters into the clamps into the sector formed by the p. 435
anterior lateral plate and the triangular and lower lateral outgrowths of the middle basic plate. The clamp also does not have the shape of a sucker or cup in the normal state.

The clamps of *Diclidophora* are arranged more complexly than any of those studied by us (Fig. 306). Here we observe the merging of the basic middle plate with one of the anterior lateral and this merging takes place in such a way that the large part of the space between these plates is occupied by a thin membrane which departs from the middle and at the same time adheres to the edge of the lateral plates in such a fashion that only a small oval opening remains in the lower part of the single plate which was formed between them (Fig. 306, II). Apparently, the described membrane corresponds to the strongly developed triangular membrane of Heterobothrium. The remaining chitinous plates are more or less symmetrical. The muscular cluster enters into the clamps through the oval opening which was indicated and apparently attaches to the interior surface of the membrane. Usually the clamp is in the half-closed state, forming an oval, slit-shaped aperture.

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[1] The drawing of the clamp of this species by Price (Price, 1943a) is incorrect; closer, but also inaccurate is the description and drawing in the work of Nagibina (Nagibina, 1953).

[2] In addition to the described structures, among all Diclidophoridae just as *Diclidophoropsis* there are chitinous sticks lying in a fixed order on the interior surface of the posterior valve of the clamp which is similar among different species. In separate cases, in addition to that, more or less well-developed thorns can be formed on the exterior surface of the interior valve, as for instance in *Diclidophora denticulata* (Olsson, 1876).

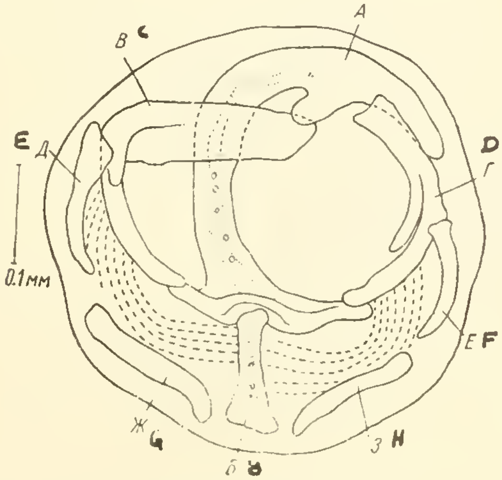

Fig. 304. Choricotyle pagelli (Gallien), attaching clamp of an Sparus centrodontus (Delar.) near the western shore of England (Atlantic Ocean). Explanation in text.

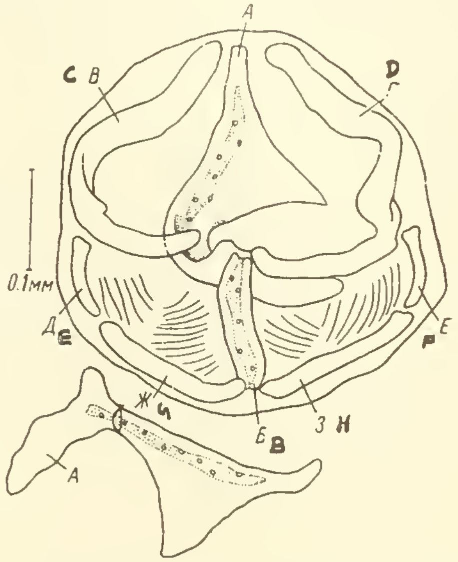

Fig. 305. Heterobothrium affinis (Linton), the attaching clamp of an adult worm from the gills of Atherestes evermanni J. and St. from the region of the Cape of Navarin (Bering Sea). Explanation in text.

One must say that the majority of the drawings of the skeletal formations of the clamps reproduced by various authors in their works leave much to be desired. Nevertheless in Cerfontaine and Yamaguti and also in a number of others the descriptions of the clamps of different species of Diclidophoridae are quite correct. During the study of the literary data we see that the peculiarities of the structure of the clamps of the separate genera described by us are observed in all their species or at any rate in all well-described ones. Exceptions apparently depend on the inaccuracies of the studies of the corresponding species. Thus, Gallien (Gallien, 1937) represents the chitinous elements of the clamp of p. 436

Diclidophora minor (Olsson, 1868) in the shape of separate, more or less symmetrical and different parts. During verification on our own actual material, the identity of which to the material of Gallien does not occasion any doubt, it was found that even in this, the smallest form of *Diclidophora* the structure of the clamps is typical for the present genus. The structure of the clamps in the genus *Cyclobothrium* is not clear. Thus, judging by the drawings and the descriptions of Goto (Goto, 1894), *C. sessilis* Goto has clamps arranged exactly according to the same principle as in *Diclidophoropsis*, whereas Yamaguti (Yamaguti, 1938) represents the clamp of this type as very similar to the type of *Heterobothrium*. At the same time, according to the drawings of the author, the clamps in *C. iniistii* Yamaguti and *C. semicossyphi* Yamaguti resemble the clamps of *Choricotyle* more closely. In all probability the clamps of *Cyclobothrium* have an asymmetric structure but nevertheless are closer than anything else to the clamps of *Diclidophoropsis*. As regards the genus *Echinopelma*, according to the description of the author the clamps of its representatives have a structure close to the one of *Choricotyle*, but differing by the presence of a special round plate lying close to the place of entrance of the cluster of muscles. It is possible that this plate corresponds to the three-pointed membrane of *Heterobothrium*.

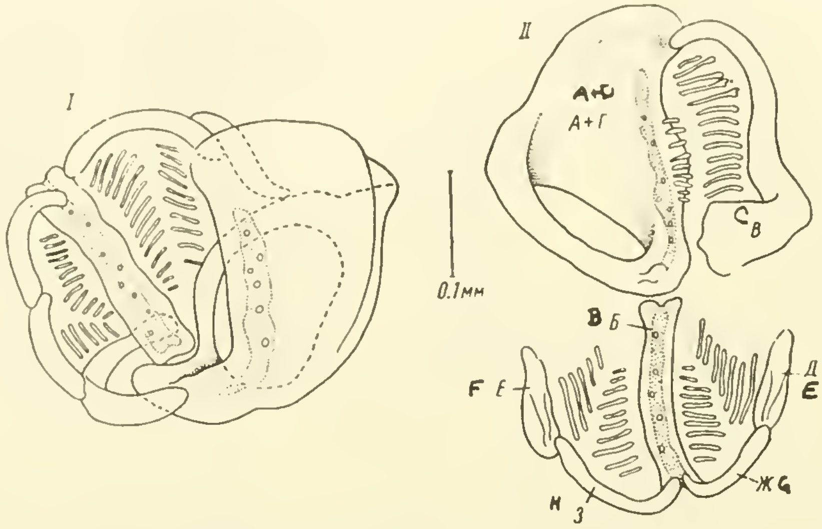

Fig. 306. *Diclidophora denticulata* (Olsson) attaching clamp from an adult worm from the gills of *Pollachius virens* (L.) from the Barents Sea; I--Chitinous parts of the attaching clamp in natural position; II--Chitinous parts of the attaching clamp cut into and unfolded; on the top is the anterior valve on the bottom is the posterior valve. Explanation in text.

Finally, one can only say about the structure of the clamps of *Pedocotyle* that Price (Price, 1943a) indicates that they are similar to the clamps of *Choricotyle cynoscioni* (MacCallum, 1917), i.e., they have in this fashion an asymmetric structure.

In spite of a varying degree of clarity concerning the structure of the clamps of Diclidophoridae, the question about their action is not fully understandable as we have already indicated. Without any doubt the clamps of *Diclidophora* act in a pinching fashion, which is recognized by all researchers. Further, in spite of the descriptions of Price (Price, 1943a), the clamps of *Heterobothrium affinis* also are real pinching formations. We have especially collected a number of samples of this species together with the gills on which they sit, and as a result of the observations of the nature of the correlation between the clamps and the tissues of the gills it is apparent that here the typical pinching action similar to *Diclidophora* takes place. This is clearly shown on the corresponding drawing (Fig. 307). However, apparently during the attachment of these worms to a flat surface [for instance to the surface of the buccal cavity where Linton observed them (Linton, 1898)] attachment proceeds both by way of pinching p. 437
as well as by way of supplementary suction similar to the one that takes place (see below) in *Diclidophoropsis*. The attachment of *Choricotyle* is obviously the same as *Diclidophora* and in separate cases a second method is also possible--simultaneous pinching and sucking action of the clamps. Again this depends upon the place of attachment of the corresponding species. As regards *Diclidophoropsis* we can firmly say that they are able to attach themselves to the body of the host with the aid of the pinching-sucking method, if as we have observed, they are located on the surface of the buccal or gill cavity and not on the gills themselves. Thus, on the anterior surface of the gill cavity of *Malagocephalus laevis* (Lowe) from the Atlantic Ocean near the shores of Ireland we have discovered more than 10 samples of *Diclidophoropsis tissieri* Gallien, 1937. The worms were located in such a fashion that a part of their clamps retained almost a maximum opening, whereas the other was half-closed. With this, obvious traces of their attachment remained on the skin of the host when the worms were removed. During the examination of these traces it was apparent that the exterior

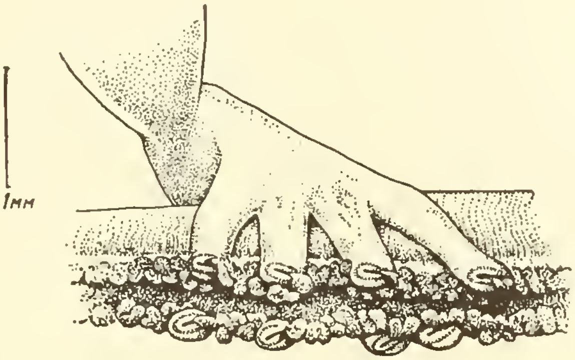

Fig. 307. *Heterobothrium affinis* (Linton), posterior end of the body on the gill filament of *Atherestes evermanni*, J. and St. from the region of the Cape of Navarin (Bering Sea).

edge of the clamp cuts itself into the tissue of the host and acts as a vise, cutting out the tissue in such a fashion that it occupies a considerably greater space inside the clamp than at the place where the clamp adjoins the body. If one cuts the entire tissue which was drawn into the cavity of the clamp he will see a more or less ovally outlined area. In addition, to that, the part of these tissues drawn into the clamp is divided into four parts corresponding to the four sections formed by the chitinous elements. With this it is fully understandable that the imprints of the two anterior sections, i.e., those fixed by the anterior valve of the clamp, appear as being cut out the most. On the cross-sections through the drawn tissues we can observe that each sector has the appearance of a regularly convex papilla which indicates the presence of suction and not just a mechanical grasping during pinching.

From what has been said before, one can conclude that the presence of either pinching action of the clamps or of a simultaneous pinching-sucking one is characteristic for all Diclidophoridae. With this the significance of either method increases not so much from the peculiarities of the structure of the clamp but from the substratum to which the attachment takes place. In other words, the clamps on the gill filaments bascially act as clamps, whereas on the surfaces of the cavities of the gills and of the mouth the sucking function sharply increases. Hence, the division into two subfamilies according to the present characteristic will hardly bear criticism and is not taken into consideration by us even though it be tempting, for the genus *Diclidophora* parasitizes gadoids, whereas *Choricotyle*--the Perciformes.

The interrelationships of the genera are not quite clear, undoubtedly the genus *Diclidophora* is more specialized and morphologically complex, whereas *Diclidophoropsis* is closer to the initial ancestral forms, which is substantiated not only by the structure of the attaching apparatus but also by the presence of two vaginal apertures. The genus *Choricotyle* occupies a position closer to *Diclidophora* than to *Diclidophoropsis*. This also pertains to the genus *Heterobothrium*. On the other hand, it is probable that *Cyclobothrium* is more primitive than the last genus and is closer to *Diclidophoropsis*. *Pedocotyle* stands somewhat apart. Apparently this genus represents a deviation from the general type of development. In a certain measure its structure is interesting from the point of view of convergency with Hexabothriidae. Because of some analogous peculiarities in the nature of attachment, one can think that here takes place a lack of development of the first pair of clamps. Finally the characteristics of the genus *Echinopelma* cause considerable perplexity. It is undoubtedly close to p. 438
Choricotyle but the presence of a single vaginal duct differentiates it from this genus if one considers that *Choricotyle* does not have a vaginal duct as is commonly accepted. However, one must think that this is possibly incorrect even though in all résumés it is written that *Diclidophora* does not have a vagina (Price, 1943a, Sproston, 1946, and others). Despite

this, Cerfontaine (Cerfontaine, 1895c) showed that in *D. denticulata* (Olsson) the vagina is precisely the same type as the one described for *Echinopelma* (see Raecke, 1945). It is also possible that the genus *Choricotyle* or its separate species likewise have a small vagina leading from the *receptaculum seminis*, and then perhaps the proximity of *Echinopelma* and *Choricotyle* will appear to be even more considerable. This is made more probable because of the fact that *Echinopelma* was described with insufficient accuracy. Thus, in spite of a rather detailed representation of the ducts of the sex system in *E. bermudae* Raecke, the *ductus genito-intestinalis*, which undoubtedly exists, was not shown.

5. Family Microcotylidae Taschenberg, 1879

(Figs. 8, 9, 23, 40, 60, 66, 75, 78, 93, 105, 113, G,
H, 125, 235-260, 308, 309)

Discocotylinea, middle or large sizes. The attaching apparatus consists of 2-3 pairs of hooks which can be absent among adult forms and of numerous (more than 4 pairs) clamps of the discocotylid-type. Usually there are one pair of edge and 2 pairs of middle hooks. More seldom the latter are represented by one pair. The attaching clamps are located on a more or less separated disc or along the edge of the body, sometimes extending anteriorly above the level of the ovary. As a rule the clamps lie symmetrically along the edges of the disc and their number is more or less equal on both sides, more seldom their number is considerably larger on one side than on the other and finally they can be located in one asymmetric row in relation to the axis of the body. The sizes of the clamps vary; usually the largest clamps are in the middle of their row. The anterior end has more or less developed cephalic glands lying in three groups, The buccal cavity has relatively powerful suckers. The intestinal trunk is two-branched. Its branches merge with each other at the posterior end of the body forming more or less numerous lateral and internal outgrowths and internal anastomoses along its length. The male sex aperture and the aperture of the uterus open for the most part into a common sex atrium. The latter is often armed by a different number of small chitinous hooks. The copulatory organ is armed or unarmed. As a rule the testes are follicular, numerous; the ovary is flask-shaped and usually curved into the S or reversed R (perhaps? U-shaped) shape. Vaginal ducts exist, more rarely they are absent. Their openings are either single or more seldom double, they lie on the dorsal side below the level of the sex opening. The uterus is pipe-shaped or often sac-shaped and as a rule contains a large number of eggs, more seldom it contains one egg at a time.

Parasites of marine (as an exception fresh water) fishes. Basically encountered on Perciformes and more seldom on Beloniformes, Mugiliformes, and Polynemiformes.

Type genus, *Microcotyle* Beneden and Hesse, 1863.

In addition to the type genus, into the composition of the family enter *Gotocotyle* Ishii, 1936 (?); *Microcotyloides* Fujii, 1944; *Gonoplasius* Sandars, 1944; *Diplasiocotyle* Sandars, 1944; *Pyragraphorus* Sproston, p. 439 1946; *Cemocotyle* Sproston, 1946; *Axine*, Abildgaard, 1794; *Neoaxine* Price, 1945; *Axinoides* Yamaguti, 1938; *Heteraxine* Yamaguti, 1938; *Lintaxine* Sproston, 1946; *Metamicrocotyle* Yamaguti, 1953; *Heteromicrocotyle* Yamaguti, 1953. Price (Price, 1936) also places *Bicotylophora* Price, 1936 here.[1]

First of all, it is indispensable to note that the type and most numerous genus, *Microcotyle*--as well as *Gotocotyle* are artificial, uniting at the present time not only representatives of different only partially described genera but possibly also representatives of a neighboring family, Gastrocotylidae. The reasons for this lie in the very inaccurate description of the attaching armature of the species under consideration, and this is true not only of authors of the past and the beginning of this century but also of a number of contemporaries. Because of this, it is indispensable to make a partially complete re-examination of all the species described to the present time. Unfortunately we do not possess sufficient material at the present time and because of this we are forced to retain the genera *Microcotyle* and *Gotocotyle* in their contemporary scope and can only indicate certain basic lines along which differentiation proceeds. As an example of the incorrect inclusion into the genus *Gotocotyle* of a species which clearly does not belong here, one can cite *G. acanthura* (Parona and Perugia, 1896) from the gills of *Brama raii* (L.) which was discovered by us during the study of Mediterranean fishes in the region of Naples. During verification, this species was found to have a structure typical for the genus *Lithidocotyle* Sproston, 1946 (Family Gastrocotylidae--see page 445), and henceforth should be renamed *L. acanthura* (Parona and Perugia, 1896) Bychowsky, *comb. nov.* The type species of *Microcotyle*, *M. donavini* Beneden and Hesse, 1863, is characterized by the symmetrical structure of the disc which is delimited from the body of the animal. With this, in adult animals the disc never extends anteriorly beyond the level of the posterior testes. Judging by the data of Sproston (Sproston, 1946), it is characteristic that the chitinous hooked armature, absent during adult forms, disappears (is sloughed off), apparently during relatively late stages of development. Thus, Sproston observed the presence of hooks among individuals already having 12 pairs of clamps (see page 214). As regards the clamps, they are of typical discocotylid structure and are

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[1] *Pterinotrema* Caballero, Bravo-Hollis and Grocott, 1954, is also ascribed by the authors to this family. We cannot say how correct this is because we do not have the description of this genus in our hands.

strictly symmetrical, and this refers also to the clamps of their right and left rows as well as the clamps within the limits of each row. The sex atrium of M. donovini is large with a large number of chitinous hooks, the copulatory organ is apparently unarmed. The united vaginal ducts open by a mid-dorsal aperture deprived of armature. One can accept that the present structure with the variation in connection to armature of the sex openings is characteristic for a very large group of species of Microcotyle, s. str. Along with this, we have a number of species of this genus with somewhat different structure. Thus, first of all one should note that the attaching disc can be of a clearly different nature. A number of species, as for instance the one which is at our disposal, M. trachini Parona and Perugia, 1889, bears a disc which is not delimited from the body but represents its extension posteriorly. The clamps lie posteriorly from the termination of the intestinal branches and of the vitellaria. In other words, if the first group of species can be characterized as forming a fold on the ventral side extending anteriorly (anterior end of the disc), then the second does not form p. 440
this fold (see Fig. 308). Finally, in the third group, to which pertains, for instance, M. gotoi Yamaguti, 1894 (sic) is related the disc is not completely delimited from the body just as among the preceding group but, so to speak, extends anteriorly along the edges of the body up to the level of the ovary or somewhat below it (Fig. 247). Practically it is difficult to speak even about an independent disc, this is rather a posterior edge of the body bearing the organs of attachment. Between these two groups apparently there are also transitional forms as for instance M. truncata Goto, 1894, which occupies the intermediary position between the second and third groups. One must note that, inasmuch as it is known to us, the symmetrical structure of the clamp persists in a majority of species pertaining to all groups. Along with this there are species among which asymmetry is obvious, which is expressed in the acquisition (development, nobis) of the mirrorness (detailed bilateral symmetry, nobis) of the right and left rows of clamps and also in the change and general complication of the clamps depending on their inception and growth, i. e., from the posterior end toward the anterior. Thus, according to our observations on individuals obtained from Pagellus mormyrus L. from Naples, M. mormyri Lorenz, 1878, has symmetrical clamps and typically "discocotylid-type" in the first (posterior) part of the disc and then during their further growth the middle clamps acquire asymmetry by way of the thickening and the merging of separate parts of the lateral arches lying exteriorly from the body (Fig. 309). Thus, this group of clamps is mirrored in relation to each other from the right to the left sides of the disc. On the very top end of the latter (anterior, nobis) where the new clamps are incepted, they again have in the beginning smaller sizes and "discocotylid" shape.

In addition to the peculiarities of the structure of the attaching disc of Microcotyle one can notice serious differences in nature of its vaginal ducts and their exterior openings within the limits of this genus in its contemporary scope. If in typical species there are 2 vaginal ducts

which later merge with each other and form a single one leading anteriorly toward one more or less rounded dorsal aperture, in addition to that structure we observe all transitions toward 2 completely separate vaginal ducts opening by independent apertures. Thus, in *M. seriolae* Yamaguti, 1940, the paired vaginal ducts extend up to the level of the common vaginal opening and approach it from the sides independently without merging with each (Yamaguti, 1940). In *M. canthari* Beneden and Hesse, 1863, the paired vaginal ducts terminate in 2 lateral independent openings. Similar relationships can be observed also among other species and particularly in an un- p. 441
described species of *Microcotyle* of the same type which we have. Without any doubt one can consider the presence of 2 vaginal openings as more primitive for the given group and thus the forms which have it as more ancient. This also corresponds with the simpler structure of the attaching disc. In these forms the second type of the latter is present for the most part. One can hardly consider either the presence of the armature of the sex atrium or the vaginal openings as primary. All these are secondary characteristics and thus the species of *Microcotyle, s. str.*, appear as the most specialized. It is most probable that it will be necessary to reconstruct later the system of the present genus as a result of the peculiarities which have been indicated. The development with the characteristic casting-off of the part of the disc with the hooks as well as the inception of the first pair of clamps during the embryonic period, as takes place in *M. mugilis* Vogt, 1878 (see page 206), also shows considerable specialization of *Microcotyle*. In connection with this it is possible to consider that *Gotocotyle* is a more primitive genus because its representatives retain the hooked armature of the disc during their entire life. However, not everything is clear for us in this genus. The descriptions of Meserve (Meserve, 1938) and Ishii and Sawada (Ishii 1936; Ishii and Sawada, 1938) are not very accurate and the structures of the clamps of the forms described by them remains unclear. It is most probable, however, that, just as in *G. acanthura* the remaining species, i.e., the entire genus, should be transferred into the family Gastrocotylidae; however, it is not possible to do this without special verification from the actual material.[1]

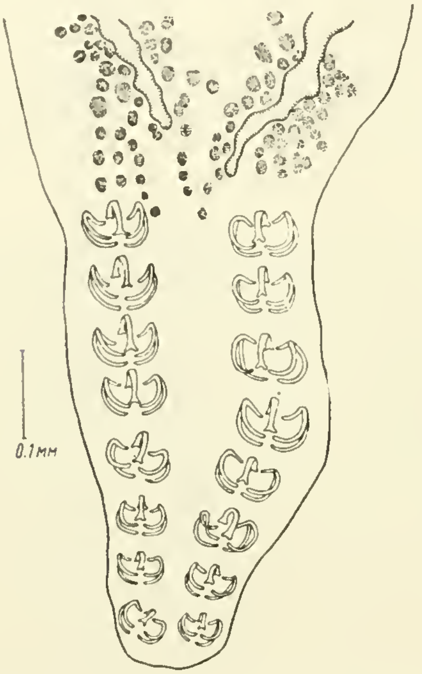

Fig. 308. *Microcotyle trachini* Parona and Perugia, posterior end of the body of an adult worm from the gills of *Trachinus radiatus* Cuv. from the Bay of Naples from the Mediterranean Sea.

The presence of only one pair of middle hooks in all species attracts attention. This is undoubtedly a very important characteristic which shows a considerable difference of this genus from Microcotyle, even in case this genus should remain in the present family. The genera

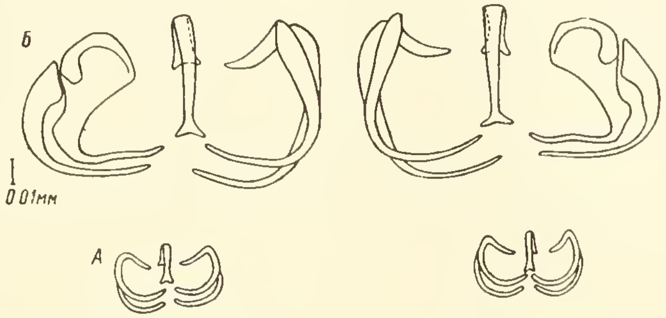

Fig. 309. Microcotyle mormyri Lorenz from the gills of Pagellus mormyrus (L.) from the Bay of Naples (Mediterranean Sea). A--Normal clamps from the right and left halves of the posterior part of the attaching disc; B--Asymmetrical clamps of the anterior part of the disc.

Microcotyloides and Gonoplasius, representatives of which we did not have, closely approach Microcotyle, in connection with which we cannot evaluate their independence with certainty. Nevertheless in all probability the separation of the first genus is fully founded because the presence of the lateral opening of the single vaginal canal is a sufficiently important p. 442 characteristic. As regards the second, in spite of the long diagnosis of the author (Sandars, 1944a) the differences from Microcotyle practically can only be summed up by the presence of a large number of glandular cells of the anterior end of the body which hardly appears sufficient, as Sproston correctly points out (Sproston, 1946).

In the further process, the presence of the differentiation of the attaching apparatus, similar to the one which is observed in M. mormyri Lorenz, leads to the formation of species with the sharply expressed two types of clamps. Their first part, incepted earlier, retains discocotylid traits, whereas the second becomes completely different. We observed a corresponding structure of the clamps in two genera Pyragraphorus and Cemocotyle, which were quite correctly separated by Sproston (Sproston, 1946) from the genus Microcotyle, s. str. The first genus is characterized by the fact that the modified clamps acquire a long "handle" which acts as a spring and resembles very much a waffle iron in appearance and the second by the growing and elongation of the customary elements of

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[1] Should this turn out to be true, it will be necessary to bring the genus Lithidocotyle near to Gotocotyle with corresponding conclusions.

the clamps. At the same time, in Cemocotyle the asymmetry of the disc is also observed: One edge bears a small number of typical clamps, whereas the second--approximately the same quantity of typical ones and in addition to that a considerable number of metamorphosed ones. One must also note that Pyragraphorus is closer to Microcotyle both by the absence of chitinous hooks as well as by the interior structure, whereas Cemocotyle is somewhat further removed because it has 3 pairs of typical hooks on the posterior end in the adult state, that is, it retains more primitive traits.

In certain relations, the genus Cemocotyle is close to Heteraxine which, however, has no chitinous hooks in the adult state. The last genus is undoubtedly very close to Microcotyle, s. str. and differs basically by the asymmetry of the disc (not clamps!) which on one side bears a very small, and on the other a considerable number of clamps.

The genus Diplasiocotyle, material of which we did not have, is very odd. Judging by the description of Sandars (Sandars, 1944a)[1], this genus has a symmetrical disc equipped with a small number of clamps of distinctly different sizes. Thus, the first, (posterior) pair of clamps has the sizes of 0.062 x 0.044 mm whereas the size of the remaining pair fluctuates from 0.250 x 0.187 to 0.437 x 0.312 mm. One can suppose that a similar development of clamps is connected with certain peculiarities of attachment during the early stages of the development of the worms. The interior structure of the only species of this genus is apparently very close to Microcotyle, s. str. The author describes 2 "suckers" on the dorsal side of the body but does not indicate their connections with the vaginal ducts which probably takes place. Certain peculiarities of the development of Diplasiocotyle (see page 216) speak for a considerable specialization of this genus.

The asymmetry of the disc of Microcotylidae, about which we have often spoken, arises in all preceding genera at the irregular or uneven development of its right and left halves depending on changes in the number of clamps located on it. With this the clamps themselves lying on both halves of the disc, are either completely alike or mirrored to each other, and the sizes of the clamps on both sides do not differ from each other. In contrast to this there are two more types of asymmetry of the p. 443
disc in Microcotylidae: 1) by way of the formation on one side of large and on the other side of small clamps; 2) by means of "unfolding" of both rows of clamps into one line in such a way that the posterior end of the disc of the larva is in the middle of one continuous row of clamps lying at a more or less sharp angle to the longitudinal axis of the body of the animal. The

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[1] Cited according to Sproston, because we did not see the present work.

clamps can be so located that according to their orientation it is impossible to say where the morphological middle of the disc is located, and the latter can be determined only by the complex of chitinous hooks retained near it.

The first of the types of asymmetry described here is characteristic for Lintaxine. This monotypic genus is separated by Sproston (Sproston, 1946) on the basis of the very indefinite data of Linton (Linton, 1940). Judging by the information of the latter, this genus has a number of large clamps on one side of the disc,while on the other side an almost double number of correspondingly smaller clamps is located. We also had one species of Microcotylidae which has not yet been described and which resembles Lintaxine very much by the given peculiarities, but differing by the presence of chitinous hooks on the posterior end of the body, which are absent in the type genus, judging by the work of Linton which has been cited. One can suppose that the appearance of asymmetry and of the disc of such a type is connected with the development of strict orientation in the disposition of the worms according to the cross-section through the gill arches of the host, i. e., by their attachment in the cavity on the wide surface of the gill filaments.

The last of the types of asymmetry of the disc indicated is characteristic for 3 genera, Axine, Neoaxine, and Axinoides, differing from each other mainly by small peculiarities of the structure of the sex system. Besides the general principle of the structure of the attaching disc,three genera also are united by the presence of one vaginal duct opening either at the side of the body (Axine, Neoaxine) or on the dorsal side (Axinoides). Monticelli (Monticelli, 1903) separated the special subfamily Axininae in which he included the genus Axine and the genera Pseudaxine and Gastrocotyle, which now enter into another family, In a special article,Price (Price, 1945) considers the question about the genus Axine and accepts the subfamily Axininae in the scope of three genera, Axine, Neoaxine, and Axinoides. We do not consider that it is possible to agree with this at the present time and rather favor the views expressed by our collaborator U. A. Strelkov who especially examined the question about the status of Axine in the system of monogenetic trematodes (Strelkov, 1953). Nevertheless,we should note that the 3 above-mentioned genera are interesting by the fact that, having an undoubtedly secondary structure of the disc in comparison with the typical Microcotylidae, they at the same time have numerous primitive traits in the structure of the sex system and particularly in the simpler vaginal tract which has already been mentioned. As regards their interrelations with each other, the genus Axinoides is the most primitive and Axine is the most specialized. With this the specialization apparently basically proceeds along the lines of oligomerization of the separate elements of the female sex system.

Price (Price, 1936) attributes the genus Bicotylophora, separated by him, to Microcotylidae without indicating any basis, however. This seems incorrect to us, for although the attaching disc of the only species, *B. trachinoti* (MacCallum, 1921), strongly resembles the microcotylid-type, the discovery of a whole series of individuals of this species on *Trachinotus carolinus* (L.) in the Gulf of Mexico U.S.A. speaks for the independence of this species and genus which is apparently related to Anthocotylidae.

6. Family Protomicrocotylidae Poche, 1925. p. 444

(Fig. 89)

Discocotylinea, having middle sizes. The attaching apparatus consists of a disc, sharply delimited from the body which bears one pair of edge hooks, 2 pairs of middle hooks and 4-6 weakly developed clamps of discocotylid-type lying on the ventral side of the posterior end of the body in one or two vertical rows. The vaginal duct is single, opening outwardly from the right intestinal trunk. The remaining characteristics are similar to the ones of Microcotylidae.

Parasites of marine Perciformes (Carangidae and Sciaenidae). In addition to that they are indicated for Clupeiformes, undoubtedly erroneously (see page 228).

Type genus, *Protomicrocotyle* Johnston and Tiegs, 1922.

In addition to the type genus, two more genera--*Bilaterocotyle* Chauhan, 1945 and *Lethacotyle* Manter and Prince, 1953, enter into the composition of the family.

This family appears mysterious to us in a number of relations. We were not able to obtain the material and consequently the subsequent analysis is based on rather incomplete and apparently not very accurate descriptions of two genera of *Protomicrocotyle*[1]--*P. mirabilis* MacCallum, 1918 and *P. pacifica* Meserve, 1938, the only species of *Bilaterocotyle*--*B. chirocentrosus* Chauhan, 1945, and *Lethacotyle fijiensis* Manter and Prince, 1953. First of all, what is most obvious is the considerable similarity between *P. pacifica*, *B. chirocentrosus*, and *L. fijiensis*, greater than between the first of these species and *P. mirabilis*. As regards such an important characteristic as testes, which judging by the data of MacCallum lie behind the ovary in the latter species, whereas in the first three they are in front of it. If the data of MacCallum are not erroneous it is possible that we will have to raise the question of dividing the genus *Protomicrocotyle* into two.

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[1] We did not have the description of P. *celebensis* Yamaguti, 1953.

The presence of a sharply individualized disc bearing hooks is characteristic for all species. With this,both the disc itself and the hooks lie in a bilaterally symmetrical fashion on it, which undoubtedly bears the primary character. Apparently the disc of the adult forms corresponds to the larval one which has grown strongly in the postembryonic period. In *Protomicrocotyle* and *Bilaterocotyle* attaching clamps of the usual discocotylid-type lie above the disc on the ventral side, whereas in *Lethacotyle* they are totally absent (Manter and Prince, 1955). The clamps are located in one row and there are 4 of them all together in *Protomicrocotyle*, whereas in *Bilaterocotyle* there are 6 lying in two vertical rows by 3's. The drawings of Meserve, 1938 show that there is a special zone around the clamps strongly resembling the embryonic tissue which forms around the clamps of *Microcotyle* in the process of development. Nevertheless,we do not have sufficient basis to suppose that we deal here with underdeveloped individuals in spite of the fact that this is indicated by the relatively small sizes of the clamps in comparison with the middle hooks of the disc.

It is very interesting but strange that in *B. pacifica*, *B. chirocentrosus* and *L. fijiensis* there is a slit-shaped depression of unknown
origin on the side of the body and somewhat above the disc which gives the
body a sharply asymmetrical appearance. Just what it constitutes is not
clear. Judging by the drawing of MacCallum (MacCallum, 1918a), *P.
mirabilis* does not have this depression. The internal structure of the last
species resembles that of *Microcotyle*; however, the vaginal duct is single,
armed and apparently located in the same way as in both other species. As p. 445
has already been indicated, the correlation between the testes and the ovary
is characteristic of the latter.

As a whole, one can say that the representatives of the present family are undoubtedly very aberrant forms having a number of primitive traits on one hand and the elements of "embryonization" on the other. We think that their separation into an independent family is justifiable although demanding further substantiation. At any rate, one can say with certainty that the attribution of the genera of Protomicrocotylidae to Valisiinae (=Anthocotylidae in the present work, see page 426), as is done by Sproston in her résumé is not supported.

7. Family Gastrocotylidae Price, 1943

(Figs. 7, 3-12, C)

Discocotylinea, of middle and large sizes. The attaching apparatus consists of 2 (?) to 3 pairs of hooks and of numerous clamps. Usually there is one pair of edge and 2 pairs of middle hooks located on the posterior end of the disc, more seldom one pair of middle hooks lies on the disc itself closer to its upper terminal or even on the lower end of the body. It is possible that sometimes one pair of middle hooks (and the edge ?) hooks completely fall off. The clamps are of a type similar to the discocotylid but differ by the presence of a number of supplementary chitinous structures. In the first place they have 2 transversal rod-shaped plates lying between the lateral parentheses of the posterior valve of the clamp. The vaginal duct apparently is always single and opens by a dorsal pore. The remaining characteristics are similar to the ones of Microcotylidae.

Parasites of marine Perciformes, predominantly Carangidae, Scombridae and other close families. One genus is known from Mugiliformes.

Type genus, *Gastrocotyle* Beneden and Hesse, 1863

Into the composition of the family also enter *Allopseudaxine*, Yamaguti, 1943, *Pseudaxine* Parona and Perugia, 1890, *Pseudomicrocotyle* Sandars, 1947, *Pricea* Chauhan, 1945, *Lithidocotyle* Sproston, 1946, *Chauhanea* Ramalingham, 1947, and *Thoracocotyle* MacCallum, 1913.

The structure of the clamps, complicated in comparison with *Microcotyle*, is characteristic for the family and this complication bears a progressive character and leads to the formation of almost a continuous surface of chitinous lining, particularly in the posterior valve, similar to the one which occurs in Mazocraeidae. The clamps of *Gastrocotyle*, *Pseudaxine*, *Allopseudaxine*, *Chauhanea* and *Thoracocotyle* are fully symmetrical whereas in *Pricea*, *Pseudomicrocotyle* and *Lithidocotyle* they acquire a sharply expressed asymmetry and because of this the right and left rows of clamps are mirrored. As regards the disc itself, it also has a tendency towards sharp asymmetry. Thus, typical genera of the family, *Gastrocotyle*, *Pseudaxine*, and *Allopseudaxine*, have a disc with one row of clamps. With this in the first genus it represents so to speak the edge of the body on which lies a series of clamps extending anteriorly considerably further than the ovary, whereas in the second and third it is p. 446
delimited just as takes place in Axine. Undoubtedly there is a tendency toward asymmetry in *Thoracocotyle* whereas the 4 remaining genera have more or less symmetrical discs.

The location of the middle hooks in some genera is curious. If in *Gastrocotyle*, *Pseudaxine*, and *Thoracotyle* 2 pairs of middle hooks lie in the posterior end of the body (on the other hand, *nobis*), the posterior end bears only one pair in *Lithidocotyle*, *Pseudomicrocotyle* and *Pricea*.[1] It is remarkable that in the last genus there is a second pair of hooks but it lies considerably above the disc or even behind it on the posterior end of the body. In an undescribed species of the present genus from *Scomberomorus niphonius* Cuv. and Val. from the Bosphorus, a part of the samples had a second pair of hooks approximately in the middle of the over-all length of the attaching disc. In the species described by Chauhan (Chauhan, 1945) the second pair of hooks was located somewhat above the attaching disc. One must think that during the time of development the growth of the disc takes place in such a fashion that both pairs of hooks are separated by the part of the body which develops between them. The fact that the second pair of hooks of *Pricea* is homologous to the normal second pair in *Gastrocotyle* any other genera does not arouse the slightest doubt and consequently and quandry of Sproston on this subject is not founded (Sproston, 1946). Something else is interesting here. It is quite possible that during the development of representatives of this genus and possibly also of *Lithidocotyle*, in which we could not find the second pair of middle hooks, this pair is shed just as the very posterior complex of hooks is shed in *Microcotyle* (see page 213). Thus,we have here very singular peculiarities in the process of postembryonic development in comparison with the majority of monogenetic trematodes in which the discs are armed with clamps. As regards *Lithidocotyle*, this genus is unusually similar to *Pricea* and it is quite possible that later they will be united, although we repeat that we did not find the second pair of middle hooks among representatives of this genus even with very meticulous re-examination.

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[1] What happens in *Allopseudaxine* and *Chauhanea* is not clear.

The correlations of the genera entering into the composition of Gastrocotylidae are not fully apparent. On the other hand, *Gastrocotyle* *Allopseudaxine*, *Chauhanea* and *Pseudaxine* have a more primitive structure of the clamps than *Pricea*, *Pseudomicrocotyle* and *Lithidocotyle*, and on the other the asymmetry of the part of the disc of the first is undoubtedly a secondary phenomenon. It is most probable that they are two lines of development which have diverged rather widely and this is substantiated also by the peculiarities of development of the second group.

The genus *Thoracotyle*, for which the presence of a relatively small number of testes and of considerable simplification of the structure of the sex system is characteristic, stands somewhat apart. In all probability, however, it is a secondary phenomenon. The lack of the material itself does not permit us to make any substantial conclusions relative to this genus,but it is possible that later it will have to be excluded from the present family.

Supplement

We did not include the genera *Tagia* Sproston, 1946 and *Hemitagia* Sproston, 1946, mentioned in the preceding text (see page 254 and others into

the system). Sproston includes them into Anthocotylinae (=Anthocotylidae according to our system); however, this is practically not justifiable. As regards Tagia, this monotypic genus may be attributed with equal success both to Anthocotylidae and Discocotylidae. The re-examination and clarification of the questions about the presence of hooks of the attaching apparatus among Tagia during any stages of the development is necessary. The second, also monotypic genus, Hemitagia, seems doubtful to us altogether and we think that the only discovered sample of p. 447
this genus is incomplete, having a partially torn off disc. This doubt is increased by the fact that the author of this species (Meserve, 1938) suspects the same. If it is so, then the question about the generic independence of Hemitagia galapagensis Meserve, 1938, possibly will be solved negatively.

In addition to that, in the systematic part there is no indication of the genus Allodiscocotyle Yamaguti, 1953. This monotypical genus is described by Yamaguti in a work (Yamaguti, 1953) which we did not possess, as we have said before. Inasmuch as we have divided Discocotylidae as understood by the preceding authors into several families, it is difficult to say to which of them this genus belongs. In any case, one can almost be certain that it does not belong to Discocotylidae in our understanding.[1]

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[1] Supplement to the galley proofs. Recently we received three more works of Hargis, (W. J. Hargis from his series "Monogenetic Trematodes of Gulf of Mexico Fishes." Part V. July, 1955, Trans. Amer. Micro. Soc. LXXIV, 3: 203-225; Part VIII, January, 1956, Proc. Helminth. Soc. Washington 23, 1: 1-13; Part IX, July, 1956, Proc. Helminth. Soc. Washington 23, 2: 153-162). In these works were described a number of new species, 3 genera (Neoheterocotyle Hargis, 1955, Dendromonocotyle Hargis, 1955, Loimopapillosum Hargis, 1955) and one new subfamily of Monocotylidae (sensu Price, 1938)--Dendromonocotylinae Hargis, 1955.

In the first place the fact that Hargis re-examined Hemitagia galapagensis (Meserve, 1938) and discovered that without doubt they do not have 4 clamps but 8 (see above) and that this species is extremely close to Tagia equadori (Meserve, 1938) deserves attention; thus, it is possible that the genus Hemitagia has no right to independent existence. In addition to that, Hargis describes two new species of Tagia, transfers into this genus Kuhnia otolithis Yamaguti, 1953 and redescribes both species known earlier. From his work it is apparent that the genus Tagia undoubtedly should be ascribed to Acanthocotylidae in our understanding. However, apparently the genus Tagia is not homogenous and later it may have to be divided at least into two. Attention is drawn by the clamps of T. bairdiella Hargis, 1956 which are completely identical with the ones of Pyragraphorus (Microcotylidae). This is another case of parallel development of similar structures (see page 468). Important are the materials of Hargis about Monocotylidae (s. lat.). The subfamily Dendromonocotylinae described by him clearly enters into the circle of Monocotylidae (*s. str.*) and has a considerable morphological interest because of its undoubtedly secondary changes. As regards the genus *Loimoipapillosum* (*L. dasyatis* Hargis, 1955) which is described by Hargis, it sharply differs from both known genera of Loimoidae by the presence of an ovary of monocotylid-type as well as by details of the structure of the attaching disc. In spite of that, one should nevertheless recognize this genus as pertaining to the present family. At the same time it is important to note that for *Loimoipapillosum* the presence of 14 edge hooks is accurately indicated (see page 370). Finally the re-establishment of a subfamily *Axininae* Monticelli, 1903, made by Hargis can hardly be accepted because the genera united in it pertain to different lines of evolutionary development of Microcotylidae (see page 438).

CHAPTER IV

PHYLOGENETIC INTERRELATIONS OF THE FAMILIES OF MONOGENETIC TREMATODES

We now pass to the structure of the phylogenetic "tree" of monogenetic trematodes. At the present time, such structures do not attract wide recognition of systematists and morphologists. It is considered that it (the construction of such trees, nobis) is simply a speculative occupation which neither justifies the labor nor the time spent on it. However, this point of view appears deeply erroneous. We are in complete agreement with A. N. Severtsov that the elucidation of factual correlations in the phylogenesis of separate groups of animals in relation to the preceding history of the animal world is a paramount problem of zoologists. Its solution presents not only historical interest but it also clarifies to us the ways of subsequent development and in a number of cases allows us to understand not only "normal" lines of the future, but also the possibilities of their active acceleration or change. p. 448

We have already spoken about phylogenesis of Monogenoidea and noted its basic way and directions in the section which precede the presentation of the system. The problems of the present chapter lead to the specifying or clarifying of concrete lines of development and correlations among contemporary Monogenoidea. Practically, this chapter represents the phylogenetic deciphering of the system proposed by us. In addition to that, we shall then attempt, on the basis of this deciphering, to make certain general conclusions which it seems to us will be of general biological interest.

First of all, examining contemporary Monogenoidea and comparing them with the hypothetical promonogenetic trematodes which were discussed earlier, we see that closest to them are representatives of the lowest monogenetic trematodes--Dactylogyridae--and groups close to them on the one hand, and Tetraonchidae and Amphibdellatidae--on the other. All these families have a number of more primitive and more specialized characteristics; however, as a whole they stand approximately at the same level of development. At the same time, in spite of the smaller number of edge hooks and the bifurcation of the intestine, the Dactylogyridae have perhaps a somewhat larger number of primitive traits. It would seem that this provides sufficient indication that this group is more ancient as a whole and formed the foundation for all the subsequent groups of Monogenoidea, especially within the limits of the first trunk (branch, nobis) of the development of the latter. Practically, our system departs from Dactylogyridae and then passes to groups morphologically more complex. However, the analysis of the correlations of the groups and the tendencies of development show that in building the phylogenetic "tree" in such a fashion we would have made a very grave error. Dactylogyridae is one of the youngest branches of the first trunk and undoubtedly became separated rather late. This disparity between the contemporary morphological structure of the separate groups of parasites and the time of the origin, or to be more precise of their separation, makes the problem relative to the structure of the phylogenetic "tree" very complicated. Consequently, our analysis cannot be based on the morphology and embryology of the corresponding animals only but must arise from a combination of these data and the data on occurrence and history of the interrelations of parasites and their hosts, determined both by occurrence and by the nature of the origin and development of the faunistic complexes of parasites on specific groups of hosts. At the same time the materials about the life cycles and biology both of the parasites just as of their contemporary hosts must be also considered. It would be tempting to utilize the data on phylogenesis of the hosts but these data used uncritically can lead us to greater errors than purely morphological analyses, especially since the materials on the phylogenesis of the hosts arouse very great doubts of their accuracy in a number of cases. Nevertheless in spite of all these difficulties the attempt at establishment of the phylogenesis of monogenetic trematodes seems to us quite likely and in the essential traits appears to us as possible to be solved clearly enough. p. 449

During the appraisal of the basic lines of development of monogenetic trematodes, we see that their attaching armature is regular and changes in direction from the larger number of edge hooks toward the smaller. Thus, among the lowest Monogenoidea this number changes from 16 to 12 and among the highest is more or less constant, and equals 10. The tendency is towards disappearance or metamorphosis or, i.e., actually to oligomerization. It would be very tempting to attempt to build the system in the form of a single number of species changing by the characteristic of the edge hooks from the many to the few hooked ones; however, this is impossible because the materials on development point to the presence of two easily distinguishable branches. The divergence of these branches, about the size and peculiarities of which we have already spoken, took place in very ancient times. The study of the nature of the faunas of the Monogenoidea of different groups of hosts as well as the morphological analysis fully confirms this. Regardless of how one pictures the speed of the evolutionary process, one can say with certainty that the divergence between both subclasses of Monogenoidea is so great that long geological periods were required for its occurrence. Would it be possible to determine, albeit tentatively, the time of its divergence? It seems to us that this question can be solved positively. First of all it can be considered that the appearance of monogenetic trematodes as a separate class probably occurred only after the separation of fishes, i.e., approximately during the Silurian period. The supposition that Monogenoidea separated earlier is improbable because they are undoubtedly specialized parasites of vertebrate animals, the entire life cycle of which, from the very beginning, was not connected with the presence of a number of intermediate hosts as is the case (the presence of intermediate hosts, nobis) in digenetic trematodes, tapeworms,

etc. We have already written about this in 1937. On the other hand, taking into consideration that the order Chimaericolidea, the most specialized, which at the same time has a number of very primitive traits, is encountered only on chimaerids and that we do not observe any transitions between this order of Monogenoidea and the one closest to it (Diclybothridea), one can say with very great certainty that this order is connected in its evolution with the hosts approximately from the moment of the separation of the latter. As confirmation for this can serve also the extremely wide geographical distribution of Chimaericolidea with their very great poverty of p. 450
genera and species. Inasmuch as there are no doubts whatsoever that the divergence of both subclasses of Monogenoidea preceded the formation of the present order, for notwithstanding their specialization and primitive traits they are indisputably representatives of the subclass Oligonchoinea, in any case this divergency took place before the Jurassic period, because contemporary chimaerids are known from that period (Berg, 1940). However, we can make the time of divergence of both subclasses of monogenetic trematodes more precise if we take into consideration that the separation of Chimaericolidea must have preceded the separation of the second order of the trunk of Oligonchoinea--Diclybothriidea. The fact that this process took place precisely so and not otherwise is shown convincingly by the comparison of the morphology of the representatives of both orders. Actually it does not seem possible to derive diclybothriids from the structure of Chimaericolidea because the former are a secondarily simplified and regressing group in many aspects. This is understandable from what has been expressed earlier (see pages 403 and 410). Diclybothriidea, which are principally connected with the Elasmobranchii, undoubtedly descend from ancestors common to them and Chimaericolidea which parasitized some sort of fossil fishes, chimaerids or Elasmobranchii, with an equal degree of probability. Inasmuch as both are known from the Devonian (Berg, 1940), one can suppose that the divergence of both trunks of Monogenoidea should be linked precisely with this period.

At the same time, we must remember that the retention of the primary characteristics peculiar to monogenetic trematodes is characteristic for the first stages of development of the first trunk and for the second--the appearance of completely new peculiarities; of a changed attaching apparatus, representing among them a combination of the primary chitinous hooked armature and the delimiting of the muscular formation "of the sucker-clamp" around part of the hooks.[1] Actually, only the appearance of this peculiarity creates

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[1] This name is unsuitable but points to the fact that in the beginning there was an organ which provided the ability of attaching by both means--suction and pinching (just as takes place among Diclidophoropsis see page 437).

Oligonchoinea in the real scope of the group because the mere oligomerization of the part of the hooked apparatus does not indicate the principal difference from the initial forms although it has a very great significance. In other words, there is a sharp difference in the nature of the development of the initial and then partially also of the subsequent, stages of formation of both subclasses--in the Polyonchoinea we deal with the normal process of oligomerization of the primary attaching apparatus; whereas in Oliogonchoinea--with new formation which take place at the locations of the apparatus with a stabilized quantity of edge hooks. Taking into consideration that these are different means of adaptation to the same thing, i.e., --attachment to the body of the host and primarily on the same places, one cannot fail to notice that the solution of the same physiological problem proceeds along different directions. Hence the correctness of the considerations of V. A. Dogiel about the nature of the interrelations between oligomerization and the other means of progressive evolution is clear.

We pass now to the examination of the correlations within the limits of separate trunks (branches, nobis) of development, i.e., of the subclass of Monogenoidea. The first trunk, i.e., Polyonchoinea, consists of 3 orders; Gyrodactylidea, Tetraonchidea, and Dactylogyridea. The first two are characterized by the presence of the attaching armature, consisting p. 451 of 16 edge hooks and a third of 14 and even partially of 12. This forces us to suppose that the first are closer to the initial ancestral forms, judging by the present characteristic. However, this does not give us the right to speak with certainty about their greater antiquity. In order to make corresponding conclusions, let us examine all the 3 orders in sequence. Thus, Gyrodactylidea consists of 3 families of which one--Sphyranuridae--clearly separated from Polystomatidae recently, as was indicated by us earlier (see page 401). Thus, Gyrodactylidae and Polystomatidae belong to the initial discussion as groups which have arisen prior to the third family. Beyond any doubt the divergence between the two families is ancient, it arose before Gyrodactylidae acquired the ability of viviparousness and the Polystomatidae acquired contemporary peculiarities of the attaching apparatus. Thus, the branch of Gyrodactyloidea takes its origin in more remote times than the families which compose it. Taking into consideration that Polystomatidae could appear, as we wrote earlier, almost simultaneously with the separation of contemporary Amphibia, one can think that this process took place approximately in the beginning of the Cretaceous period or the end of the Jurassic. This is substantiated indirectly also by the data about Gyrodactylidae, which are historically younger than Polystomatidae and became separated most probably somewhat earlier than the separation of the contemporary Salmonoidei (see page 124). Inasmuch as the latter can be considered as having arisen not later than the Paleocene period (Osmeridae on which part of Gyrodactyloidea is encountered, undoubtedly separated as early as the Cretaceous period, see Berg, 1940), the data reproduced on Polystomatidae and Gyrodactylidae are sufficiently trustworthy. Let us suppose, however, that our conclusions are erroneous and that the branch of Gyrodactyloidea appeared at a much later period. Then we will have to suppose that in the first place the Gyrodactylus-like ancestors of Gyrodactyloidea transferred to parasitizing Salmonoidei at a certain period when this group already had reached its full development. This supposition is possible, but then the relatively narrow adaptability (specificity, nobis) of this genus to a determined circle of hosts of very wide geographical distribution which gives, one would think, the possibility of contact with many other fishes of the same superfamily (see page 308), becomes unclear. In the second place, the widest (practically world-wide) distribution of Polystomatidae under the condition of the unusual adaptability of the life cycle of separate species of parasites to their hosts speaks for the indubitable antiquity of their interrelations; furthermore, the life cycle of Polystoma shows that the representatives of this genus first became adapted to life on the ancestors of contemporary Amphibia having gills during their entire life, because the transfer to parasitizing in the urinary bladder is undoubtedly a secondary phenomenon (see page 124). The supposition that the ancestors of Polystoma first became adapted to the life on the gills of the larvae of contemporary Ranidae cannot be considered trustworthy in any way, which again speaks for the probable appearance of Polystomatidae in relatively recent times (let us remember that even the contemporary genus Rana separated not later than the Eocene, whereas it is possible not to doubt the earlier appearance of Polystomatidae, for the reasons indicated above.)

Thus the suppositions about the greater youth of the branch of Gyrodactylidae contradict the facts which we have at our disposal. We especially dwell on this question somewhat more in detail in order to demonstrate the manner of our reasoning, which gives us a known certainty of their correctness even though it is based on indirect material. We shall also note along the way that interrelations within the limits of the families of Gyrodactyloidea are clear from what has been said earlier (see page 397) and p. 452
from the drawing in Figure 310 which does not require special explanations.

The second order--Tetraonchidea--presents much greater difficulties in the determinations of the correlations of the families composing it, as well as for the formation of opinion about the relative antiquity of the separation of both the families and of the order as a whole. The presence of a sac- or pipe-shaped intestine is characteristic for 3 families, Tetraonchidae, Tetraonchoididae and Bothitrematidae. There is no doubt that this is a primitive character which is not encountered in any other families of the same subclass. Thus, according to the given characteristic the fourth family of the order - Amphibdellatidae, differs already by a newer characteristic - bifurcation of the intestine. Two families, (Tetraonchoididae and Bothitrematidae) have one pair of middle hooks each and the remaining 2, two each. Although the presence of one pair of hooks is a more primitive characteristic it can have both primary and secondary origin. Because of this it is not possible to attribute great significance to it in the relation which

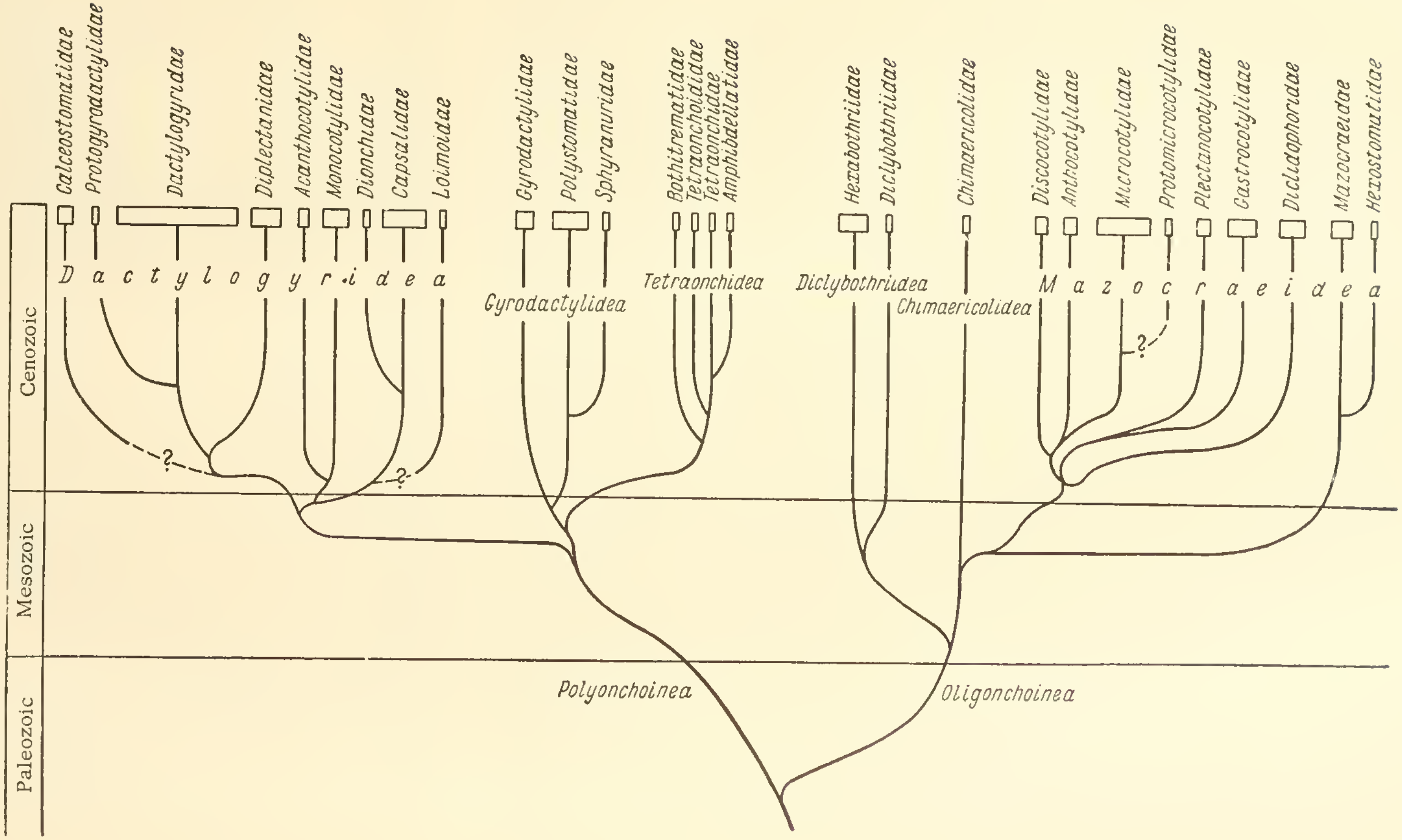
Calceostomatidae
Protogyrodactylidae
Dactylogyridae
Diplectanidae
Acanthocotylidae
Monocotylidae
Dionchidae
Capsalidae
Loimoidae
Dactylogyridea
?
?
Gyrodactylidae
Polystomatidae
Sphyranuridae
Gyrodactylidea
Bothitrematidae
Tetraonchoididae
Tetraonchidae
Amphibdellatidae
Tetraonchidea
Hexabothriidae
Diclybothriidae
Diclybothriidea
Chimaericolidae
Chimaericolidea
Discocotylidae
Anthocotylidae
Microcotylidae
Protomicrocotylidae
Plectanocotylidae
Gastrocotylidae
Diclidophoridae
Mazocraeidae
Hexostomatidae
Mazocraeidea
?
Polyonchoinea
Oligonchoinea
Cenozoic
Mesozoic
Paleozoic

Fig. 310. Diagram of the phylogenetic interrelations of the families of monogenetic trematodes. The relative size of the groups (number of genera) is indicated by the sizes of the upper rectangles. The family of Microbothriidae, the position of which in the system is not clear (See text) is not included.

interests us. The data about occurrence force us to believe that Tetraonchidae appeared not earlier than the Cretaceous period and not later than the Oligocene period (see page 308); Tetraonchoididae, Bothitrematidae and Amphibdellatidae--not earlier than the Eocene (Berg, 1940, see also pages 390 and 394). Thus the occurrence of the families of Tetraonchoidea allows us to say that apparently Tetraonchidae is the most ancient family. The remaining three appear to be younger and one should consider that Bothitrematidae and Tetraonchoididae became separated last on the basis of indirect considerations and mainly of the data on morphology. Taking into consideration that the ancestors of Tetraonchidea are undoubtedly morphologically close to those of Gyrodactylidea one can suppose that both orders having the attaching disc with 16 edge hooks are closer to each other than to the 14-hooked forms which are united by the order of Dactylogyridea. One cannot fail to note the fact that within the limits of Tetraonchidea we observe the tendency both to the preservation of the primitive attaching apparatus with insignificant changes (Tetraonchidae and Amphibdellatidae) and to the transformation of the disc into a single sucking apparatus (Bothitrematidae) and even to the peculiar division of the latter into sections by septa, and at the same time the appearance of suckers on the disc, true not at all the same as in Polystomatidae and not on the base of the primary edge hooks (Tetraonchoididae). All these tendencies lead, as we will mention in more detail later, to converging similarities of the representatives of the present family with families related to other systematic groups.

As a whole the entire order of Tetraonchidea gives the impression of not being clearly delimited and it is possible that it will require later reconstructions. Nevertheless, the peculiarities which separate it underscore its relative antiquity, whereas the differences of separate families indicate their rapid divergence from each other.

On the basis of what has been expressed in the preceding sections, the question about the time of the appearance of the third order, Dactylogyridea, is solved relatively easily.

One can speak with certainty that the ancestral forms of this order appeared later than the ones of Gyrodactylidea but undoubtedly somewhat earlier than Tetraonchidea; in other words, the separation of this order can be considered most probably linked with the Cretaceous period.

In conclusion, the question about the separation of separate orders of Polyonchoinea is solved rather unexpectedly. Although the order Gyrodactyloidea appears to be the most ancient, possessing the greater p. 454
number of edge hooks of the attaching disc, the second order--Tetraonchidea, which possesses the same peculiarity, is younger than Dactylogyridea which have the 14-hooked attaching apparatus.

Before speaking about correlations within the limits of the order Dactylogyridea we must direct attention to the important break which occurs in our data concerning the time of separation of the trunk of Polyonchoinea from Oligonchoinea on one hand, and on the other-- about the supposedly more recent time of the appearance of some of the orders of the first subclass. We have said above that the separation of both subclasses of both Monogenoidea took place most probably in the Devonian and have just established that all three orders of Polyonchoinea appeared not earlier than the end of the Jurassic period at best. Thus, a huge span of time passes between the appearance of the differentiated ancestors of the separate orders of Polyonchoinea and the time of divergence of the trunk of Oligonchoinea, by which we judge the divergence of both trunks, What happened during this period? First of all one can think that there is a mistake in our present considerations, namely that the separation of the trunk of Oligonchoinea from the common "tree" of Monogenoidea does not indicate that Polyonchoinea also became separated in the same period. It is quite possible that the separation of the first took place by means of a quick change in the structures (new formations!) of promonogenetic trematodes; whereas the process of oligomerization, characteristic for the formation of Polyonchoinea, proceeded considerably slower. One can even suppose that after the separation of Oligonchoinea, the trunk which lead to Polyonchoinea was already characterized by forms which had a larger number of edge hooks than the Gyrodactylidea and Tetraonchidea. It is understandable that all is a region of pure speculation however, one can consider it as an indubitable fact that the primitive ancestors of Polyonchoinea, whatever structure they may have had, existed for a relatively long time on some sort of fishes which have not persisted to the present time, and it is also possible, on Selachii which already inhabited the fresh and marine bodies of water at that period.[1] A similar break also takes place between the time of the separation of the 16-hooked forms and the appearance of the first Tetraonchidea. Here again one can suppose an extended period of existence of the primary undifferentiated Tetraonchidea on fishes different than the ones that are their hosts at the present time and most probably which have died out subsequently. The latter supposition is based on the fact that it is improbable that the species living on fishes which exist until the present time became extinct on them. Such a case is theoretically possible but practically could hardly have a mass character (primary significance, nobis). Theoretically its probability is based on the possibility of a sharp change of conditions of the host and subsequently of its parasite, of the survival of the first during the death of the second. However, all our data indicate that usually Monogenoidea are not less enduring than their hosts and perish either at the same time with them or even, as is often the case (in artificial conditions), after them (see experiments of Shulmann, page 79).

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[1] This enables us to suppose that the study of the fauna of Monogenoidea of Selachii and particularly on the more primitive sharks which have not yet been studied (Heterodontidae and Chlamydoselachidae) can add many supplementary materials for a clearer understanding of the phylogeny of the monogenetic trematodes.

However, let us return to Dactylogyridea. The morphological analysis of this order forces us to divide it into 2 sufficiently distinct separate suborders--Dactylogyrinea and Monopisthocotylinea. The analysis p. 455 of occurrence of the representatives of these suborders shows that the first are peculiar only to Teleostei, whereas the second parasitize both these fishes and selachians. With this, the analysis which was cited in the preceding chapters gives us reason to believe that the basic part of the families of Monopisthocotylinea are encountered on Selachii indicates them to be their initial parasites and apparently very ancient ones. Hence, the supposition that the second suborder and not the first is more ancient in the time of separation becomes quite probable, although, repeating what has been said about it, morphologically the first is considerably closer to the supposedly ancestral forms. It will be better, however, to express the considerations about the possible time of separation of both suborders after the examination of the connections of separate families within the limits of each suborder.

Dactylogyrinea represents a more compact group than Monopisthocotylinea. Two families which enter the composition of the first suborder, namely Dactylogyridae and Diplectanidae, are characterized by the presence of 14 edge hooks of the attaching disc, while two others--Protogyrodactylidae and Calceostomatidae, have only 12 edge hooks. However, as has already been mentioned before (see page 360), there is strong basis to doubt the correctness of the presence of only the 12 hooks on Protogyrodactylidae, it is more possible that they also have 14 hooks just like the Dactylogyridae, with which they are very close and with which they are closely linked genetically, independently of the solution of the question about the quantity of edge hooks. There are all necessary indications to suppose that this family descends directly from Dactylogyridae and even definitely from Ancyrocephalinae and thus it is relatively young. Taking into consideration that Protogyrodactylidae are encountered only in Australia and only in freshwater Serranidae one can consider that they separated no earlier than the Eocene period. All the other families of the suborder undoubtedly are of more ancient origin and thus Protogyrodactylidae is historically one of the youngest families of Monogenoidea.[1]

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[1] This once more shows how unfortunate it was to name the group as was done by Johnston and Tiegs.

We should undoubtedly also recognize Calceostomatidae, having the 12-hooked attaching disc, as a relatively young family. As we have already indicated (see page 274), it is distributed very singularly both on marine and fresh water fishes, and it is possible it is an artificial one, but at the same time the Paleocene period should probably be considered as its earliest period of appearance. Morphological peculiarities of the typical representatives of the Calceostomatidae show that during the development of certain progressive traits characteristic for this family, the process of oligomerization of the chitinous apparatus is characteristic, which is expressed not only by the disappearance of one pair of edge hooks but also in the simplification of the middle hooks and of their connecting apparatus which disappear even among part of the genera (see page 361). If one is to take into consideration and reject this tendency in development, we can nevertheless speak about the considerable proximity of Calceostomatidae to Dactylogyridae. Both families undoubtedly originate from very close if not from common ancestors.

As was already indicated (see page 355) the family Diplectanidae is somewhat more removed. Undoubtedly this progressive branch is characterized by a number of neoplasms (new formation, nobis). Taking into account the occurrence of Diplectanidae almost exclusively on the Perciformes and even more precisely on Percoidae, one can think that separation of this family took place not earlier than the Paleocene and most probably p. 456 somewhat later. Apparently the ancestral forms of Diplectanidae separated directly from Dactylogyridae just as among Protogyrodactylidae, or what is more probable, from ancestors common with the latter. Certain traits, sharply distinguishing Diplectanidae from Dactylogyridae and not permitting us to derive the first from the second, speak for this supposition. In the first place, the characteristic structure of the ovary which is not encountered in Dactylogyridae is attributed to these traits.

As regards the most numerous family, both from the generic and specific point of view, Dactylogyridae, it undoubtedly occupies the phylogenetically central position in the suborder. The interrelations between the subfamilies of Dactylogyridae are not fully clear. One can consider it certain that Ancyrocephalinae derived from Dactylogyrus-shaped ancestors; however, to link this subfamily with Dactylogyrinae would be erroneous, not only because it is possible that certain forms of the latter are derived by means of simplification from Ancyrocephalinae (see page 347), but because of the fact that the representatives of both of these families have a number of morphological peculiarities which apparently developed independently among these and others from common ancestors. Consequently, one can think that both subfamilies develop more or less simultaneously and appear historically almost at the same time. The time of their appearance can be determined by the fact that the former are linked most closely with Cypriniformes in their distribution whereas the latter, most probably, first appeared on Perciformes. Both hosts of the family under examination are known as fossils starting from the Paleocene, which gives some basis to suppose the appearance of Dactylogyridae approximately at the same time, also. The third subfamily--Linguadactylinae, which apparently has a shorter history, inasmuch as it is linked with Gadiformes to which its ancestors undoubtedly transferred from the Perciformes, forms an exception. Thus, as a whole the family Dactylogyridae represents a relatively young group which attained rather strong development in the post-Paleocene period. As regards the interrelations of the separate genera comprising the families, they are understandable from the preceding text (see pages 346 - 355).

In conclusion, as we have just analyzed, Dactylogyrinea as a whole represents a complex of families descending either from each other or from very close or from common ancestors of the Dactylogyrus-shaped type. There is no doubt that such also were the ancestors of the second suborder, i.e., Monopisthocotylinea. This suborder has a less monolithic character, in the first place because of the fact that into it enters two sharply separated families--Acanthocotylidae and Microbothriidae. The status of the latter in the system, not only of the suborder, but of the class, is not clear to us (see page 385). Because of that they are excluded from further discussion. They can be judged only after special research on the development of their representatives. As regards Acanthocotylidae, just as Diplectanidae in the preceding suborder, in addition to possessing a number of peculiarities of internal organization they often sharply differ by the nature of the development of the attaching apparatus among adult worms, which was indicated in detail above (see page 383). Nevertheless, one can consider the separation of this branch of development from the common trunk of Dactylogyridea and in direct proximity from the beginning of Monopisthocotylinea as most probable, taking into consideration with this the primary nature of Acanthocotylidae parasitizing Elasmobranchii, almost exclusively on skates of the family Rajidae. One can think that the formation of this family did not take place before the upper-Cretaceous and most probably during the Paleocene period.

The four remaining families of Monopisthocotylinea are much closer to each other, although here also their correlations are not the same. The family of Monocotylidae is closest to the initial dactylogyrid-type. The interrelations within this family were examined in detail in the systematic part (see page 364), but as a whole this family, peculiar exclusively to Elasmobranchii, apparently separated for the first time rather long ago. One cannot say with certainty whether the first Monocotylidae appeared on sharks or skates but we can think that this family undoubtedly existed already in the Cretaceous, i.e., it separated earlier than all the Dactylogyrinea as a whole. The second large family of this suborder, Capsalidae, also examined in detail above (see pages 373 - 383), is genetically very close to Monocotylidae but is considerably younger. In spite of the fact that part of Capsalidae is encountered on very ancient Selachii this undoubtedly is a secondary phenomenon and the development of the family is linked with the p. 457

separation of Perciformes for which it is a characteristic. Hence one can suppose that Capsalidae separated approximately not before the Paleocene. Dionchidae separated from Capsalidae or from ancestors close to them (see page 272). Judging from their occurrence this took place not before the Eocene and perhaps even somewhat later. The last family of the present suborder--Loimoidae (see page 370), if indeed it actually belongs to it, has a number of such singular traits that it is not possible to doubt its very early separation from the common trunk even if it were earlier than the separation of Monocotylidae, if they are judged by their contemporary distribution on the hosts.

Thus, the second suborder of Dactylogyridea has apparently a somewhat older origin than the first in spite of the great specialization of the families which comprise it.

Thus, we have analyzed correlations within the limits of the first subclass, attempting to determine not only the limits of the separate groups which compose it but also the time of their formation. We now pass to Oligonchoinea. Of three orders composing this subclass we have already judged in detail the time of the separation of Chimaericolidea in the beginning of the present chapter. As was already mentioned, Diclybothriidea have common ancestors with Chimaericolidea. Their separation probably was very ancient. Taking into consideration that their basic progressive family, Hexabothriidae, is initially linked with Elasmobranchii and widely distributed on them, and also that it has a number of secondarily simplified peculiarities of organization one can think that the appearance of ancestors of Hexabothriidae took place somewhat before the separation of the contemporary Selachii from their extinct ancestors. Hence, taking into consideration that the contemporary Elasmobranchii are known from the lower Jurassic one can conclude that Hexabothriidae became separated at any rate not later than the Triassic. The second family of this order--Diclybothriidae is younger and undoubtedly descends from ancestors very close to the first. Taking into consideration the data about occurrence, one can suppose that its appearance approximately in the Cretaceous period is very probable.

Finally, the last, the order Mazocraeidea, very numerous in contrast to the two examined before, descends from *Chimaericola*-like ancestors beyond any doubt, and naturally falls into two suborders, apparently formed independently and thus possibly deserving elevation to a higher rank. Let us note, however, that this is not done by us for a number of reasons, (see page 417) and especially because of the insufficient study of the embryonic development of both suborders. As regards Mazocraeinea p. 458
this suborder is more ancient than the Discocotylinea. As confirmation for this serves the nature of the primary distribution of Mazocraeidea (dae? *nobis*) as well as the structure of the attaching apparatus, especially of its chitinous parts (see pages 417 and 423). It is most probable that the separation of Mazocraeidae is connected with the separation of Clupeidae,

the traces of which are known from the lower Cretaceous. The second family of this suborder, Hexostomatidae, is obviously considerably younger, its members have a number of traits indicating considerable secondary complications of a part of the system of the organs along with the reduction of the chitinous elements of the attaching apparatus (see page 421). Inasmuch as it occurs exclusively on the tunas and on the fishes close to them, Cybiidae and Carangidae, one can think that its separation took place not before the Eocene. We suppose that Hexostomatidae descend from Mazocraeidae taking their origin from some sort of Octostoma-like ancestors. This can be substantiated only after a study of the postembryonic development of the corresponding forms inasmuch as at the present time even the young immature individuals of Hexostoma are unknown to us.

The suborder Discocotylinea is divided into several groups comprising close families; however, as a whole it is sufficiently monolithic and relatively much younger than the preceding one. Discocotylidae, which shows considerable specialization,connected in all probability with the secondary adaptation to fresh waters, is the most separated of all the families of Discocotylinea, (the suborder as a whole was initially marine and only some of its species occasionally penetrate into fresh water, or continually live there with the exception of the present family). In their origin the Discocotylidae are undoubtedly connected with Anthocotylidae from common ancestors from which they are derived. We think that this took place in rather distant times because the working out of the morphological and cyclical peculiarities pertaining to Diplozoonidae could hardly develop in relatively short periods. Taking into consideration the occurrence of Discocotylidae (see page 274) and also the probable time of the formation of Anthocotylidae, one can suppose that the former separated approximately in the Paleocene period which is also confirmed by the nature of the distribution of the representatives of the family.

The 2 families--Anthocotylidae and Diclidophoridae, are very close to the Discocotylidae. Both are encountered on Perciformes as well as on Gadiformes and are connected in their formation with both of these orders as well as with Macruriformes (Diclidophoridae). Undoubtedly, these families have common ancestors and it is even possible that Diclidophoridae represents the lateral branch of Anthocotylidae. The time of separation of both families is linked with the time of appearance of contemporary Perciformes and even somewhat later, i. e., it is dated in the late Cretaceous or most likely the Paleocene. One can link the appearance of Plectanocotyle, which represents a somewhat isolated branch of the same trunk but secondarily acquiring a certain complication in the structure of the attaching apparatus (see page 428), with practically the same time or somewhat later.

Two more families--Microcotylidae and Gastrocotylidae probably became separated at the same time or approximately at the same time from the common line of Anthocotyle--Diclidophoridae on the one hand and

Plectanocotyle on the other. For both the appearance of newly formed clamps, which are similar in structure, as well as the characteristic 4 pairs of the remaining families of Anthocotylinea is characteristic (Dogiel, 1954a). They are the two youngest families of the present suborder, not counting Protomicrocotylidae which most probably separated from Microcotylidae, p. 459
although it is not possible to speak about this with certainty (see page 444).

Thus, on the basis of what has been said before we can visualize the general nature of the correlations of Monogenoidea in the form of the appended general diagram (Fig. 310). This diagram does not pertain to a great degree of accuracy, nevertheless it reflects the interrelations of separate groups and of time in a certain measure. The latter can undoubtedly arouse great doubts and possibly be subjected to very severe criticism. Nevertheless, it is impossible to visualize from contemporary distribution on the hosts (and in separate, more fully studied cases, also the geographical) that the present determination of the historical links between separate groups of parasites could be formed in a different determination of time of the separation of the separate groups, [i. e. it is impossible to visualize from their present distribution on the hosts (as well as their geographical distribution) that the nature of the historical links between the separate groups of parasites could be any other way; or, in other words, using these techniques and these data the present solution seems the only one possible, nobis]. This determination of time is obviously very relative and allows errors of many hundreds of thousands of years; however, it gives a general idea about the nature of the tempo of the evaluation of the large systematic categories of Monogenoidea.[1]

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[1] Supplement to proofreading. V. B. Dubinin drew my attention to the book of Baer, (J. G. Baer, Ecology of Animal Parasites, University of Illinois Press, Urbanna, 1952), in which the evolution of the attaching disc of the monogenetic trematodes is represented in the form of a diagram on page 118. As is clear from the preceding text this diagram does not correspond at all to reality and does not have any evolutiophylogenetic, nor relative nor comparative anatomical significance. It is interesting because it illustrates to what errors the sole examination of morphological studies alone can lead. Thus all the variety of forms of the attaching apparatus of Monogenoidea are derived from the disc of Udonella, i. e., a group which does not have a direct connection with monogenetic trematodes (see A. V. Ivanov, 1953). Furthermore, the disc of Benedenia gives origin to the one of Gyrodactylus, the disc of Tristoma to Heterobothrium etc. In addition to that, a line is extended from Heterobothrium to Polystoma and from the latter to Sphyranura. Thus, Baer does not even see the principal difference between the complex chitinous apparatus of the clamps of Heterobothrium and the suckers of Polystomatidae. Further comments seem unnecessary to us.

CHAPTER V

ABOUT CERTAIN COMMON PECULIARITIES OF PHYLOGENETIC DEVELOPMENT OF MONOGENETIC TREMATODES

If, after accepting the proposed phylogenetic scheme and the p. 460 nature of the distribution of corresponding groups of Monogenoidea on their hosts as a basis, one tries to evaluate the correlations between the antiquity of the group of the hosts and the level of organization of their initial parasites he shall obtain very interesting data. Thus, of the 6 orders of Monogenoidea accepted by us, Chimaericolidea from Oligonchoinea and Gyrodactylidea from Polyonchoinea undoubtedly appear the most specialized while at the same time having very primitive and very complex traits of organization. If the first are linked with the most ancient hosts, the second on the other hand have a wide distribution,although they are encountered primarily also on the more ancient of the contemporary Teleostomi (excluding Acipenseriformes), but with this it is possible to think that they appeared on them a very long time ago because as has already been said, the genus *Gyrodactyloides* is undoubtedly derived from *Gyrodactylus*-like ancestors and at the same time it is primarily connected with the relatively ancient group of Salmonoidei and it did not transfer on them from the highest Teleostei. The finding of Polystomatidae and Sphyranuridae on Amphibia and Reptilia, and the unusual adaptability of their life cycles to their hosts (see page 119) also speaks for the antiquity of this group, for contemporary Amphibia and Reptilia separated a very long time ago and are historically considerably older than contemporary Teleostei, with the exception perhaps of the Clupeiformes. Taking into consideration that the group Polystomatidae represents a progressively developing and very highly organized group,whereas Gyrodactylidae separated a very long time ago, because it is only they that have worked out the viviparousness which is peculiar to them, and also that it parasitizes hosts which are very ancient in their origin, one can consider that this line is the most specialized in the phylogenetic branch of the lowest Monogenoidea.

Continuing to examine both subclasses of Monogenoidea from this point of view we see quite clearly that basically the more ancient the host the more specialized the parasite. This can be attributed to the fact that the time during which the present parasite is found on the corresponding host was very prolonged. Hence,it is clear that the degree of morphological and biological specialization which determines the occurrence of a specific group of parasites on a particular group of hosts allows us to speak about a longer or shorter period of existence of both groups. At the same time, we must remember that for monogenetic trematodes specific occurrence is characteristic in the vast number of known species and consequently it would not be sufficient and p. 461 perhaps would even be erroneous to base the determination of the historical links on it. The specific occurrence and the degree of morphological specialization of the group is another matter. These data can be utilized relatively for correction

and establishment of the period (geological time, nobis) of the separation of the group. Actually if one should evaluate the orders of monogenetic trematodes from these points of view he will see full substantiation of what has been said. Without entering into details, which are quite clear from what has been said before, it is possible to say accurately that within the limits of Polyonchoinea, Dactylogyridea are the most simply organized groups followed by Tetraonchidea and finally Gyrodactylidea, and among Oligonchoinea one should place Mazocraeidae (Mazocraeidea? nobis) first, then Diclidobothriidea and Chimaericolidea. Thus, the morphological data and the analysis of occurrence lead us to conclusions which appear at first glance as paradoxical-- i.e., the older the order of Monogenoidea basically the less it resembles and the further it is morphologically from the ancestral forms. The reasons for this phenomenon, which clearly contradict the commonly accepted view about the mutual parallel evolution of the parasite and the hosts about which we have already spoken (see page 296), apparently lead us to the fact that the hosts which have a lower organization generally retain it because of insignificant changes of conditions of their existence, whereas their parasites at the beginning little adapted to them, during the long period of their presence on these hosts become adapted more and more precisely to the characteristic peculiarities of the host.
With this, the continuation of existence does not give the parasite the time to stop in the process of adaptation at a fixed level and forces it to evolve in a corresponding direction. In this apparently we can see a substantial peculiarity of the general pace of evolution of a number of parasitic organisms. Without attempting now to analyze this phenomenon as a whole, one cannot fail not to note that we also observe an analogous situation among tapeworms (Fuhrmann, 1928 - 1932).

The fact that in the analysis of the occurrence we often see transfers of contemporary species from one group of hosts to another serves as an interesting substantiation of what has been said; however, these transfers are made according to definite norms (patterns, nobis), namely-- basically they do not take place among more ancient phylogenetic groups. Thus, one cannot fail to note that Gyrodactylidea and Tetraonchidea from Polyonchoinea and Chimaericolidea and Diclybothriidea from Oligonchoinea practically do not make any transfers to any group of hosts which are not primarily peculiar to them, and if they make them, they are made only in exceptional cases and then only regressively, if one can so express himself, i.e., on historically more ancient groups (see pages 300 and 411). Thus, the ancient groups of parasites have a closer link with their hosts, which again underscores the peculiarity of the evolutionary process of Monogenoidea indicated above.

Together with this, there is another important trait in the nature of interrelations of Monogenoidea. It is the clearly expressed small quantity of species and genera in the more ancient orders, which is distinctly apparent from the phylogenetic diagram. From our point of view, the reasons for this lie in the fact that within the limits of the orders of Monogenoidea the evolutionary process took place in two ways--by way of a greater and greater specialization and of the breaking in with the adaptation toward parasitizing the same host during the period of prolonged existence of the parasite on the given, little-changing host and by way of a relatively rapid species and genus formation during the location of the parasite on quickly evolving progressive groups. In the last type of evolutionary process that p. 462 height of organization which was peculiar to the ancestral forms as a rule is preserved and the important morphological structures are not touched, whereas in the first type a slow change and transformation into the form sharply different from the initial ancestral organism takes place as has been indicated. If the second group of evolutionary changes does not provoke special doubts and corresponds sufficiently distinctly to the ideoadaptations, in the understanding of A. N. Severtsov (1922b, 1925), then the first cannot be evaluated either as an ideoadaptation or as an aromorphosis,but represents something different. We shall note preliminarily, so as not to come back to the aromorphoses, that the latter undoubtedly take place in the evolution of Monogenoidea and by them one can explain both the appearance of new orders and of new families, which in the vast majority of cases, and especially in the lowest Monogenoidea, sharply differ from each other by the degree of sophistication of the organization and the origin of new progressive peculiarities.

The fact that the gradual qualitative change in the organization of the first type of parasite does not represent an ideoadaptation is fully apparent from the fact that in this process takes place not a mere change but a considerable elevation of the life and morphological level which is characteristic for aromorphous changes. However, this is not aromorphosis in the pure state, for rapid reconstructions of the organization under the influence of sharp changes in the condition of existence are characteristic for the latter, a circumstance which is absent in our case. However, the very fact of the presence of such changes demands considerable supplementary confirmation. For that reason, let us permit ourselves to depart from our basic theme and dwell on certain general questions.

It is commonly accepted at the present time that the process of species formation bears an adaptive character and takes place as a result of interrelations between the exterior and the interior factors of development in which selection plays an important role in the formation of the new. However, if this is basically accepted by all, when it comes to the evaluation of the meaning of the separate factors, the opinions sharply diverge. Hence the exaggeration of the role of one of the factors and the underevaluation of the rest or even practically their denial. We are inclined, however, to think that for the correct evaluation of each factor one must pay greater attention to the organism as a morphophysiological whole and not to its separate structures which represent it neither separately nor totally.

As regards the exterior factors and their role in species formation, very much has been said about them lately. One can consider that the underevaluation of their role which took place in the past has now been outdated although even now the nature of reaction of the organism to the exterior influences is not sufficiently clear. One must think that the complete adequacy of the morphophysiological reaction, as this is propagandized at the present time by many, hardly occurs here. For us however, is not this question which is interesting, but the question about interior factors of development and in this connection about the material with which natural selection deals. Strange as it may seem, the question about automotion of the living material which is rather sufficiently analyzed in other regions of knowledge and which represents the basis for the dialectical understanding of the world is clearly underestimated in biology. It is accepted that under the influence of the exterior factors the organism gives a countless quantity of most various departures from the initial type as was first shown by Darwin. However, this can hardly be accepted as the only p. 463 possible solution, actually we have a number of factors showing that the change of organisms can take place only in a strictly determined direction and that the quantity of principal variations available is distinctly limited. Practically this is shown to us by the numerous regularities (or norms, nobis) of the evolutionary process, in particular the ones which were laid on the foundation of the theory of homologous series which were worked out by Soviet scholars (N. I. Vavilov, 1920, 1935), concerning oligomerization of homologous and homonymous organs (Dogiel, 1936, 1952, 1954a), concerning the principle of polymerization (Dogiel, 1929) we think that the changeability of organisms, which has a phylogenetic significance in a number of cases, is far from being so unlimited and can be sharply circumscribed by the peculiarities of the automotion (self-moving, self-direction, nobis) of the living material which possesses, at a given stage, such a structure as enables it to change only in a determined direction. Thus, we recognize the presence of clearly oriented evolutionary changes. In the opinions of V. A. Dogiel on the present question, with which we are in complete agreement, these exist. Hence, it is quite clear that the meaning of selection in our opinion is much more delimited than is usually accepted. We are not stopping in detail on these questions, inasmuch as they have a completely independent interest and demand a special, sufficiently detailed research. The conditions which have been indicated were cited here only to make clear our principal views on the given question because this is indispensable for what will follow.

If one accepts this point of view, it is fully understandable that the change of the species in a strictly determined direction under weakly changing exterior conditions, just as we accepted in the cases of Chimaericolidae, Diclybothriidea and so forth, is possible. The consideration about the fact that contemporary species represent the remnants of groups which had powerful development in the past can be cited as a confirmation to our conception of the development of these groups; however, although such a thing is quite possible, it can hardly explain those peculiarities of distribution on the hosts and the degree of morphological differentiation which were indicated in the preceding text. If one accepts the last point of view it will be completely obscure why Chimaericolidae, for instance, did not transfer peculiarities of the structure of their sex system to Mazocraeidae or Diclybothriidae, although undoubtedly both last groups descend from the trunk of Chimaericolidae ? The fact that the given peculiarity appeared after the branching off of both younger branches, i.e., that which served as the basis of our considerations, can serve as the only explanation.

Let us return, however, to the further analysis of the details of the phylogenetic scheme. The commonly accepted view is that biological progress on the basis of morphological regressive development is characteristic for parasitic animals. Monogenetic trematodes cannot serve in any measure as substantiation for these views, quite to the contrary, their evolution as a whole is built on the progressive development of morphological structures. This is understandable because the basic changes in structure concern two systems of organs--attaching and sex. Nevertheless, in separate cases regressive processes take place in one just as in the other. As regards the attaching apparatus, these cases are relatively few and embrace entire systematic categories for the most part. Let us note along the way to avoid misunderstanding that we do not consider the normal process p. 464 of oligomerization of edge hooks as the indication of morphological regression, although at first glance the decrease in the number of hooks should be understood precisely as such. However, taking into consideration that this is a special qualitative difference and fully distinctly expressed process, we exclude it from consideration in the present case. We see regressive changes of the attaching apparatus present among very few Dactylogyridae (reduction of middle hooks in some genera, or more rarely, species of Capsalidae, Dactylogyridae, Calceostomatidae), in Sphyranuridae from Gyrodactylidea, in Hexostomatidae from Mazocraeidea, and finally in the entire order Diclybothriidea. As regards regressive changes in the sex system they bear a different nature and concern separate private peculiarities--chitinous armature of the copulatory organ etc. Thus, the reductions of the sex system do not have any principal significance and do not characterize more or less separated groups. Let us note also that in speaking about reductions we must differentiate between them and the underdeveloped particular structures, although this presents considerable difficulties in separate cases.

The general progressive nature of the development of morphological structures, connected principally with fully determined adaptive tendencies (see page 324) causes numerous convergent similarities within the limits of this class. We have already written several times about separate cases of their appearance (Bychowsky, 1933b, 1949, 1959; Bychowsky and Gussew, 1955; Bychowsky and Nagibina, 1954); however, chiefly only individual cases were discussed and this problem was not envisaged more widely--within the scope of the entire group. But the examination of greater material shows that the nature of the developing convergencies is very different and deserves more meticulous attention.

First of all we can distinguish convergencies of homologous and non-homologous organs and structures. For instance, the undoubtedly converging similarity of the secondary disc of Acanthocotylidae (see page 383) with the primary discs of other monogenetic trematodes can serve as an example of the latter. Likewise, thesucker-shaped pulvilli of Tetraonchoididae (see page 31) are very similar to the suckers of Polystomatidae, however, they have a different origin than the latter. The number of similar cases could be considerably increased; however, they are completely understandable by themselves and also in their greater part they are generally sufficiently coarse and superficially evaluated from the point of view of their origin and evolutionary significance. Convergencies of homologous organs are much more complex and interesting. Among them we observe similarities peculiar only to one specific structure or system of formations, to separate organs or a number of them both linked with each other as well as not connected functionally. With this we have a whole gradation of convergencies by degrees of phylogenetic proximity of species possessing correspondingly similar peculiarities. Speaking about separate structures, one can point to the structure of the middle hooks in a number of Dactylogyridae. Their origin can be interpreted differently; however, their homology to each other does not arouse any doubts. The appearance of a special indented fracture on the interior edge of the curvature of the point of the middle hooks is characteristic for many representatives of the genus Dactylogyrus. Often this break also finds its reflection in a small thickening of the exterior edge of the point and then the hook acquires a special indented edge. Nevertheless there are no doubts that this peculiarity arises each time independently in a number of cases. Thus, it is peculiar to D. varicorhini Bychowsky (Fig. 311, A) which was found on middle-Asian Varicorhinus spp. probably linked with each other in their origin, but it appears (also, nobis) p. 465
in D. markewitschi Gussew (Fig. 311, B) from the Amur fishes, Saurogobio dobryi Bl., not connected in any way with the middle-Asiatic species.

In addition to that, in the genus Falciunguis there is a very similar change in the initial part of the hook (Fig. 311, C); the representatives of the genus Dogielius (Fig. 147) are arranged analogously. The first of these genera is clearly of Eastern, apparently Chinese origin, and the second middle-Asiatic. The genetic links of their hosts are also very remote (the first is known from Cyprini and the second from Barbini). Just as the case of Acolpenteron and Pseudacolpenteron, discussed in the work of Bychowsky and Gussew cited above, the examples cited here pertain to closely related species in one genus or of close genera of the same family.

However, there is a more striking example of analogous changes of the middle hooks, not within the limits of one family but among the representatives of various subclasses. Thus, in a number of cases in the middle hooks there appears a special wing- or spur-shaped outgrowth along their edges somewhat above the point which serves apparently as a supplementary adaptation for more firm attachment of the hook in its penetration into the tissues of the host. This characteristic, peculiar to one species of Dactylogyrus (D. pterocleidus Gussew, 1955) is encountered among representatives of the genus Urocleidus (=Pterocleidus of authors) (Mueller, 1936; Mizelle, 1938), and in one more as yet undescribed genus close to Anchylodiscoides which was discovered by us on an Indian fish (Pseudotropius garua H. B.).

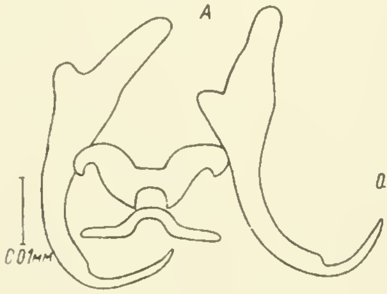

Fig. 311. Middle hooks of certain Dactylogyridae. A--Dactylogyrus varicorhini Bychowsky from the gills of Varicorhinus buhsei (Kessl.) from the rivers of Iran; B--Dactylogyrus markewitschi Gussew, from the gills of Saurogobio dabryi Bl. from Lake Hanka; C--Falciunguis parabramis Achmerow, from the gills of Parabramis pekinensis (Bas) from the Amur River.

However, in addition to these cases which exist among the representatives of the same family, Dactylogyridae, just as the preceding ones, the same peculiarity in the structure of the middle hooks also exists in a number of (all?) species of the genus Pricea Chauhan (see Chauhan, 1955 and also Figure 312), i. e., among representatives of Gastrocotylidae far removed from Dactylogyridae as is clearly apparent from the phylogenetic diagram. The examples cited indicate that a particular chitinous structure very often (but not always) can show completely identical changes in the adaptation to analogous conditions of existence independently of the degree of phylogenetic proximity of the hosts. It seems to us that here takes place not simply a converging similarity of homologous structures, but the manifestation of those internal structural possibilities about which we have spoken somewhat earlier and to which we draw attention only because of the singularity p. 466
(uncommonness) of their distribution and their relative rarity of appearance. The explanation of the appearance of such peculiarities by summarizing in (or, conjecturing that they are?, nobis) unoriented variations seems to us to be a longer stretch than the attempt to understand it as a verification of the internal structural peculiarities of a given morphological form.

Attaching formations not taken separately but as particular systems produce singular converging similarities. As a good example in this connection are the cases of adaptation of the attaching apparatus of certain lowest Monogenoidea for the embracing of the gill filaments of the host, which have a specific length, by the system of middle hooks. This adaptation is especially characteristic for Diplectanidae among which the 3 connecting plates are extremely elongated and form an almost inflexible support, fixing 4 middle hooks lying in pairs along the side of the disc at a particular distance from each other. This distance is determined by the width of the gill filament. Convergently similar structure is acquired by the attaching apparatus of certain Dactylogyridae where the middle part of the system consists not of 3 but only of one primary middle connecting plate and the edges not of 2 but only of one pair of hooks. For instance Dactylogyrus singularis Gussew (Gussew, 1955) has a similar structure. Likewise the strengthening of the system of middle hooks leads to converging similarities among the genera Tetraonchus (Tetraonchidae) and Actinocleidus (Dactylogyridae). In the first genus one middle plate is located between the 4 middle

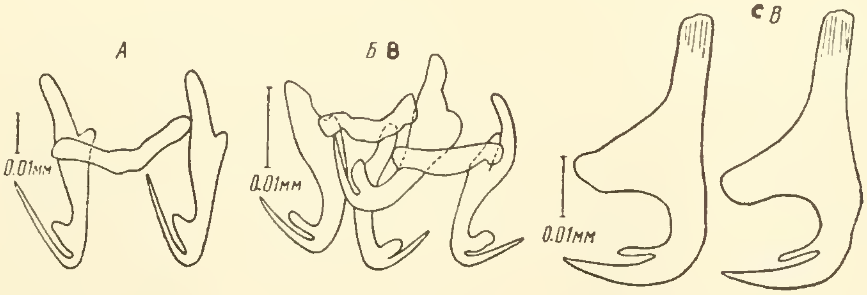

Fig. 312. Middle hooks of certain Dactylogyridae and Gastrocotylidae. A--Dactylogyrus pterocleidus Gussew from the gills of Erythroculter oxycephalus Bl. from the Island of Hanka; B--Urocleidus acer Mueller from the gills of Eupomotis gibbosus L. from the U.S.A. (According to Mueller, 1936); C--Pricea sp. from the gills of Cybium guttatum (Gil.) from the Java Sea.

hooks, whereas in the second--2. However, in the last case these two plates are connected constantly with each other by means of special outgrowths and apparently without any capability of movement,[1] forming a single two-faced plate which in the end (in the last analysis, nobis) plays the same role as the connecting plate of Tetraonchus with which it has a considerable exterior similarity. One must attribute also the indubitable similarity in structure of the disc of Acanthocotylidae and of the "plectans" (or plaque, nobis) of Diplectanidae to the same category of facts (see page 384). At the same time, the similarity is expressed not only in the common nature of origin of secondary attaching disc or discs above the primary, but also in the nature of the location of p. 467 chitinous structures and also, in separate cases, in the form of the latter (see Figs. 181 and 313). It is interesting to note with this that the similarity between Acanthocotylidae and Diplectanidae, however, is not only in this structure, but also in the nature and location and the form of the ovary. In both families the ovary is singularly retort-shaped and among representatives of both families its extended terminal part loops around one of the trunks of the intestine, a peculiarity not widely distributed among Monogenoidea.[1] Together with this, both families pertain to different suborders of Dactylogyridae (sic), and the absence of direct links between these does not arouse any doubts.

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[1] We did not have live material at our disposal, only fixed.

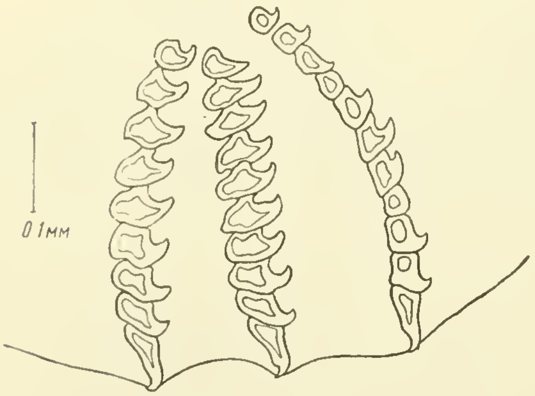

Fig. 313. *Acanthocotyle williamsi* Price, part of the chitinous plates of the secondary attaching disc of worm from the skin of *Raja rosispinus* G. and Town. near the eastern region of southern Sakhalin (Sea of Okhotsk).

One can think that the origin of the septa on the attaching disc of Monocotylidae and Capsalidae undoubtedly took place independently of each other; this is even more probable for Dionchidae. Thus, similar structures of the transformation of homologous organs are the result of the height of organization (the degree of advancement of organization, *nobis*) and their converging nature. We shall note along the way that one can also attribute the appearance of septa of the attaching disc in Tetraonchoididae, which are rather far removed from both the above mentioned families, to the same category of facts. Convergent similarities of similar order arise not only in progressive development, but also in the processes of morphological regression. Thus, this is well apparent in the example of the change of the attaching apparatus in Hexabothriidae, Diclybothriidae and Hexostomatidae. For the first, the disappearance of the chitinous armature during inception of the first pair of clamps chronologically, is characteristic, as is their transformation into suckers which have only a muscular nature. Inasmuch as the posterior part of the disc retains insignificant sizes, whereas the anterior one strongly grows, an impression is formed that the disc bears 3 pairs of clamps or suckers. In Diclybothriidae, among which the posterior part of the disc retains very inconsequential remnants of the clamps, their chitinous parts acquire even greater similarity with the 6-suckered forms, basically in contrast to the first family. This process is especially advanced in *Paradiclybothrium* in which, as is known, the posterior part of the disc almost does not develop and the entire disc has a distinct appearance of 6-clamped or rather of the 6-suckered one. An analogous process, it is true not extending very far, is observed also in Hexostomatidae. But by chance the name of the order does not correspond to the actual number of the attaching clamps! Thus, with certain differences in the processes of reduction, all 3 families acquire common traits in the structure of the attaching disc and become similar to Polystomatidae. This similarity already bears the nature of a more coarse p. 468 convergence which, however, was utilized in the systems preceding ours for the evaluation of the systematic status of Diclybothriidea. Let us remember also that in Polystomatidae and Sphyranuridae, which represent the highest link of development of Polyonchoinea, the *ductus genito-intestinalis* appears completely independently as a result of special conditions of reproduction similar to the ones of Oligonchoinea among which this characteristic is peculiar to the entire group as a whole.

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[1] An ovary of similar shape and location exists also in a number of Monocotylidae.

There is still one more genus among the highest monogenetic trematodes in which, for reasons completely unknown to us, one pair of clamps is absent and this results again in converging similarity with the above-mentioned families. This genus, *Plectanocotyle*, pertains to a special family and what is especially interesting is that the genus *Octoplectanocotyle*, which is the closest to it and unusually close in structure, has a completely normal development of the attaching apparatus and in addition to that lives on the same host and is encountered in the same location as *Plectanocotyle*. On the basis of the structure of both genera, one may think that an insufficient development of the fourth pair of clamps takes place in the latter. The opposite example of considerable growth of the anterior pair of clamps among two genera independent of each other, *Anthocotyle* and *Pseudoanthocotyle* was described by us with L. F. Nagibina relatively recently (Bychowsky and Nagibina, 1954).

Returning to the cases of progressive development of homologous and homodynamic organs, one must consider one more example. As was indicated before, the 4 normal pairs of clamps peculiar to the basic mass of Oligonchoinea are developed on the base of the part of the edge hooks which in corresponding cases enter differently into the composition of the chitinous base of the clamp. Along with this, within the limits of Mazocraeidae (Mazocraeidea?, *nobis*) two groups, Microcotylidae and Gastrocotylidae, are observed, in which a new progressive formation of another row of pairs of clamps takes place. The fact that this is a new formation was correctly indicated by V. A. Dogiel in his work on oligomerization (Dogiel, 1954a). Nevertheless, all the clamps of these worms are homodynamic and homonymous to each other and to the clamps of the remaining Mazocraeidae

(Mazocraeidea?, nobis). However, the numerous consecutive inceptions of the clamps takes place independently of each other in both families, for Gastrocotylidae, as is apparent from the phylogenetic diagram, descends from Plectanocotylidae, and Microcotylidae from the ancestors of Discocotylidae--Anthocotylidae. Exceedingly interesting was the discovery of the representatives of the new genus[1] on the flying fish Prognicthis agoo (Schleg.) during the expedition on the Vityaz in 1955 in the Pacific Ocean which is close to the typical Diclidophoridae in its structure but has an attaching disc equipped not with eight clamps, as is characteristic for the present family, but with 18. Thus, the tendency toward the new formation of a larger number of clamps appears within the limits of one more branch of Mazocraeidae (Mazocraeidea?, nobis), again completely independently of both preceding cases.

Drawing certain conclusions about the questions under consideration concerning convergent similarities within the limits of the group of monogenetic trematodes we can note that, in the first place, only those cases have undoubtedly phylogenetic significance where convergencies arise within the limits of homologous and homonymous structures, and in the second place the appearance of convergent peculiarities of characteristics in closely related groups leads to wide parallelism which is conditioned p. 469
both by common conditions of existence as well as the internal potentialities for the development of specific structures. It seems to us that the study of the convergencies, in the wide sense of this phenomenon, and especially the study of parallelisms must give very valuable and important results both in the study of phylogeny of separate groups of animals and in the understanding of common principles of the evolutionary process. The materials which have been expressed above, it seems to us, give certain support to the present conclusions.

In closing we must underline that a whole number of our opinions demand further refinement and corrections. Nevertheless, we think that the basic traits of the proposed phylogenetic scheme and the evaluation of phylogenetic tendencies in Monogenoidea will remain relatively unchanged in the future.

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[1] The description of this genus and the elaboration of its systematic status will be given in a special work.

CHAPTER VI

THE POSITION OF MONOGENETIC TREMATODES IN THE SYSTEM OF FLATWORMS

We now pass to the discussion of the question of the position of p. 470 monogenetic trematodes in the system of flatworms. Our considerations on this subject were expressed in an article in 1937 devoted to correlations of ontogenesis and phylogenesis of parasitic flatworms. In this work is given a short historical survey of views on the origin of parasitic flatworms, and it is indicated that monogenetic trematodes were joined by different authors to different groups. In particular, according to D. F. Snitsin (Snitsin, 1911) Monogenoidea descend partially from digenetic trematodes by means of simplification of their life cycles. Conversely, Janicki (Janicki, 1921) considers that monogenetic trematodes, descending from Rhabdocoela, gave rise to digenetic trematodes. The last point of view is most widely distributed (Meixner, 1926, and Fuhrmann, 1928-1932, and others). As regards the flatworms, their direct connection with monogenetic trematodes was recognized only by Spengel (Spengel, 1905), whereas the remaining scholars considered them as descending directly from straight-intestined Turbellaria. During the consideration of the interrelations of monogenetic trematodes with digenetic ones we came to the conclusion that the contemporary data on morphology, development and life cycle of these groups do not provide any basis to suppose the commonness of their origin. The existing similarity in the structure of Monogenoidea and hermophidic mature digenetic trematodes is a purely converging phenomenon which does not in any way indicate their actual phylogenetic consanguinity. As regards the interrelations between the tapeworms and the digenetic trematodes, we have indicated the complete correctness of Fuhrmann's point of view who considers the rapprochement of both groups as impossible. As a result we came to the conclusion that digenetic trematodes are very far from Monogenoidea and Cestoidea, in connection with which we thought it necessary to divide monogenetic trematodes and digenetic trematodes into two independent classes. Passing to the consideration of the interrelations between tapeworms and monogenetic trematodes we have purposely stopped on the question of the status of Gyrocotylidae, which relates to Cestodaria according to the system commonly accepted at that time. As is known, the question about the orientation of the body of these peculiar worms had not yet been completely solved at that time and considerable discussions were going on on the subject of which of their ends was homologous to the anterior end of the rest of tapeworms. In the work of Ruszkowski, which came out in 1932, it is shown with sufficient basis that the posterior end of Gyrocotylidae is the one which is p. 471 equipped with the rosette and bears embryonic hooks during the time of development, characteristic for the lycophore of these animals. In connection with the clarification of the proper orientation of the body of Gyrocotylidae we were forced to examine their morphological and histological structure more attentively. This re-examination led us to the unexpected conclusion that this group should be considered as a completely independent class of parasitic flatworms and not as a family entering into the composition of the subclass Cestodaria of tapeworms. At the same time, the peculiarities of the structure of Gyrocotylidae are such that on the one hand these worms are undoubtedly very close to Monogenoidea and on the other--to Cestoidea and thus occupy an intermediary position between these two classes.

The researches on the development of monogenetic trematodes which were conducted by us at that time forced us to attribute a much greater significance to the larval stage and to the chitinous armature of its posterior end. On the basis of this we came to the conclusion about homology of the initial larval stages of tapeworms, Gyrocotyloidea, and monogenetic trematodes. In connection with this, and also on the basis of the somewhat re-examined theory of the cercomere of Janicki (Janicki, 1921), we established that the origin of tapeworms from Monogenoidea-like ancestors should be considered as more probable and that the intermediary group between these classes is Gyrocotyloidea. All these 3 classes represent a special branch in the development of flatworms. The presence of a cercomere in the larval stage is characteristic for this branch, in connection with which we have united them into a special superclass Cercomermorphae descending from Rhabdocoela independently of digenetic trematodes.

Such is the basic content of our work of 1937. The views expressed are completely held by us also at the present time. During the 20 years which have elapsed since then, a whole number of specialists have joined our point of view. Thus, the system which was proposed by us was accepted in a number of works of Soviet parasitologists. In addition to that, it is used by A. P. Markevich (1950, 1951) in his résumés. V. M. Beklemishev (1952) accepted it partially, he separates Monogenoidea into an independent class but retains Gyrocotyloidea in the composition of Cestoidea--Cestodaria. V. A. Dogiel in his last work, "Oligomerization of Homologous Organs as One of the Main Directions of the Evolution of Animals" (1954) also accepts the system proposed by us. It is accepted in the work, "Large Practical Work in the Zoology of Invertebrates," which is being prepared for publication under the direction of V. I. Polianski, etc.

During the current period objections to it have been expressed only by D. M. Fedotov in his survey of studies on the phylogeny of the invertebrates of U.S.S.R. during the last 20 years (Fedotov, 1938). D. M. Fedotov briefly outlines our work and then writes: "The views of Bychowsky on phylogenetic relationships in the system of parasitic flatworms are so far insufficiently substantiated by facts. He attributes principal significance to the differences in structure of monogenetic and digenetic trematodes and to the similarity--only significance as converging characteristics.

In order to underline the important meaning of the presence of the attaching disc with the hooks on the posterior end, Bychowsky bypasses the differences in the organization of the monogenetic trematodes and tapeworms, even though, be it in connection with the sex system, the differences which he himself recognizes as very considerable. If one does not count the differences in details between different systems, the entire combination of the basic traits of monogenetic and digenetic trematodes is so different from the basis of the p. 472 structure of tapeworms that it is hardly possible to divide the trematodes into two phylogenetically distinct classes and even more to unite monogenetic trematodes and tapeworms into one superclass. If ontogenesis will not give further substantiations of the similarity between tapeworms and monogenetic trematodes, it will be necessary to recognize the formation of the posterior attaching apparatus among both groups as a convergency and as an adaptive characteristic which arose in connection with the conditions of larval development of both. It is simpler to refuse recognition of the homology of the exterior characteristic than to accept a number of traits of internal structure of monogenetic and digenetic trematodes and tapeworms as convergent. The comparison of organization between monogenetic trematodes and Gyrocotylidae in Bychowsky is better founded; it is possible that he is right in bringing these groups closer together. It is hardly allowable, even in the form of a diagram, to present the picture of evolution with the indication of geological periods and the scope of the branches in different periods for forms the fossil remains of which do not exist. Bychowsky is undoubtedly right in that tapeworms should not be derived from digenetic trematodes. These groups are too specialized but, properly speaking, the monogenetic trematodes are also too specialized to be considered as the ancestors of tapeworms. There are no paleontological proofs of the great antiquity of monogenetic trematodes. Compared with tapeworms their ancestry is different and the embryology of both so far does not yield any similarities except for the early development of the attaching disc.

Further substantiation of the anatomical and embryological proximity of monogenetic trematodes is necessary for the acceptance of the phylogenetic suppositions of Bychowsky, but for the time being it is more likely to allow the origin of monogenetic and digenetic trematodes from a common Rhabdocoele ancestor. The tapeworms also descended from some sort of rhabdocoelid but their ancestors apparently were ectoparasites at first, which led to the development of strong organs of attachment among them which are comparable but not homologous to the ones among monogenetic trematodes and which now appear in the embryological developmental details in the shape of phylogenetic "remnants".

"The morphological differences between trematodes and tapeworms are great but they are obscured by the variety which is observed among Rhabdocoele turbellarians, in connection with which it is quite possible to derive a primary ancestor from this group of worms for trematodes as well as for tapeworms."

However, the objections of D. N. Fedotov seem insufficiently convincing to us. The point of departure about the proximity of the internal structure of monogenetic and digenetic trematodes understood by D. N.

Fedotov hardly corresponds to reality. The attentive reader of the first part of our work, knowing the structure of digenetic trematodes, can easily conclude that there are many more differences than similarities between Monogenoidea and Trematoda and in the first place in the most important systems of organs--nervous and sex. As regards the real similarity, they have a more general nature which embraces not only these two classes but also the remaining groups of flatworms, including the free-living ones. However, in addition to this, one must not base himself only on the morphological structure of one mature phase of the development of animals inasmuch as the appearance of a number of similarities and differences which are caused by the conditions of existence of these phases is possible. A much p. 473 greater significance should be attributed to larval phases and particularly to the entire life cycle. Comparing monogenetic and digenetic trematodes in this connection, one can be surprised, not by the fact that we divide these two groups, but that until very recently they were attributed to one class.

Among contemporary Rhabdocoela, there are some species which strikingly resemble monogenetic trematodes and others--digenetic, so that one can say almost with certainty from which each descends. Reference to digenetic trematodes with a simplified cycle of development, as for instance Aspidogastridae also cannot be taken into consideration because this very aberrant group has not yet been sufficiently studied, and their larval stages are structurally very far from the larvae of monogenetic trematodes. Thus, the independence of the origin of Monogenoidea and Trematoda, it is true from ancestors very close to each other, cannot be subjected to serious doubt, which is recognized at the present time by all researchers of flatworms. The second, and properly speaking, the basic moment of doubts of D. N. Fedotov is actually a misunderstanding. He supposes that it is inadmissible to consider Monogenoidea, a very specialized group (with which we completely agree), as ancestors also of the very specialized tapeworms. Such a formulation of the question seems to us fully justifiable but the present conclusion does not follow at all from the text of our work, on the contrary it completely contradicts it. According to our considerations the monogenetic trematodes, just as the tapeworms, descend from common primitive monogenetic-like ancestors, which doesn't mean at all that Monogenoidea gave rise to Cestoidea.

Furthermore, it seems strange to us that while recognizing more or less the plausibility of our considerations about the connections between Monogenoidea and Gyrocotyloidea, D. N. Fedotov considers it possible to speak about the inadmissibility of comparison of the internal structure of monogenetic trematodes and tapeworms. In the first place if one is to accept that the divergence of both of these classes is sufficiently great then a comparison of their internal organization should be considered only in very general traits; and in the second, if there exists a group close on one hand to one class and on the other--to another, it would be correct to draw attention not to the links but to the differences of two extreme members of one phylogenetic branch. Using a similar approach for the analysis of consanguinous ties we can arrive at very unsuccessful conclusions about consanguinous relations even among representatives of one species of animals, not to speak about larger taxonomic units. Nevertheless, a number of important peculiarities in the structures of Monogenoidea and Cestoidea (see a little further) are very close to each other and are sharply juxtaposed to the corresponding structure of Trematoda.

Finally, to suppose that the unusually striking similarities in the structure of the attaching apparatus of monogenetic trematodes and the larvae of tapeworms is a converging phenomenon as D. N. Fedatov does is hardly justifiable. The common tendencies of oligomerization, the peculiarities of development and also of morphological similarity of the chitinous elements of the cercomere of both classes give sufficient bases to consider that here occurs a commonness of origin, i. e., homology of corresponding structures. During the development of any characteristic a careful morphological analysis can always show which peculiarities are developed convergently because under these conditions one never observes absolute similarities of structures. As a matter of fact, we have already spoken about convergent similarities and, recognizing their important significance p. 474 in the development of Platoda, we cannot recognize the appearance of the cercomere in all three classes of cercomeromorphous flatworms as convergent.

In conclusion, we think that the considerations of D. N. Fedotov and his interpretation of the interrelations of the flatworms, which correspond to a formerly widely distributed opinion, are hardly justified even though they deserve attention. Contemporary materials force us to suppose that the separation of the groups of cercomeromorpha is proper and to attribute phylogenetic significance to it.

Without wishing to repeat what has already been said before, we permit ourselves nevertheless to dwell on certain new facts and considerations substantiating, from our point of view, the scheme of the interrelations of Monogenoidea with other classes of flatworms as accepted by us.

Very noteworthy is the clarification of the peculiarities of development among certain Microcotylidae among which the shedding of the posterior part of the attaching disc is observed (see page 212). This process very closely resembles the shedding of the cercomere which is characteristic for a number of tapeworms (including Cestodaria). At the same time, it is also curious that the part of the disc with 3 pairs of hooks (2 pairs of middle and one pair of edge) is shed, which numerically coincides with the ones among tapeworms. It is understandable that these 3 pairs of hooks do not correspond to the 3 pairs of hooks of the cercomere of Cestoidea (although in connection with one pair one can suppose that here exists a real homology), but the analogy is very considerable. However, greater significance should be attributed to the very fact of the shedding of the part of the disc or the cercomere caused by the changes of adaptive peculiarities in the process of individual development. Only after the establishment of the fact of the autotomy of the part of the disc in Mircocotylidae do reasons for the shedding of the cercomere of tapeworms, which appears at first a very strange phenomenon, become clear. Actually in Microcotylidae it is completely clear that the posterior (the first) edge hooks and both pairs of middle hooks, which play a leading role in the attachment of the larva during the development of more powerful attaching organs--clamps, lose their functional significance and are either retained as a remnant known to be inactive for the entire life or are completely cast off. Likewise, it is not less understandable that this process embraces only one pair of edge hooks and particularly the one lying between the middle hooks. As we have seen above, the reason for this is that only this pair is used in the formation of clamps. It is completely understandable that with the oligomerization of edge hooks characteristic for the general line of development of the edge hook apparatus and with the loss of their function autotomy of the section of the body--cercomere, which bears these non-functional remnants, takes place. At the same time, as is usually characteristic for many rudimentary formations, the interruption of the normal process is often observed for instance the retention of hooks in the body and the rejection of only a part of the cercomere deprived of the latter. All this is understandable, and one can only join the opinion of V. A. Dogiel that it is "one of the most significant discoveries in the domain of embryology of worms during the last two decades" (Dogiel, 1954a).

Among the data obtained during recent years on the structure of monogenetic trematodes, a large number appear to be important from the point of view which interests us. Thus, the discovery of the special subfamily of Diplectanidae--Rhamnocercinae (see page 355) showed the obvious error in the objections of Fuhrmann (Fuhrmann, 1928-1932) concerning the fact that the presence of complex cuticular thorns with their points directed forward contradicts the point of view about recognizing as the posterior end p. 475
of Gyrocotylidae the end which bears the rosette as (because it is a structure which is not encountered, *nobis*) the one which is never encountered anywhere else in the animal kingdom. However, we have already written about the "scales" of Diplectaninae, whose points face forward. An interesting example is cited by V. N. Beklemishev in the second edition of his work (Beklimishev, 1950); "in the larvae of the mosquito *Aedes*, swimming forward by means of their heads, the microsetae of the anterior part are oriented forward whereas the microsetae of the posterior part of the body--backward..." "Thus," writes Beklemishev, "the direction of the angle of inclination of the skin thorns is an adaptive characteristic, depending on the direction of the movement of the animal and not possessing significant constancy to serve as a criterion of the anterior end of the body from a morphological point of view." However, the example of Rhamnocercinae is interesting also from another point

of view in the sense that in this case there is no doubt of the presence of a special musculature, even though it is in part of the thorns, i.e., --a considerable similarity in structure with the thorns of the covering of the Gyrocotylidae.

During further research on the structure of Capsalinae, we noticed that the ovary in these worms, at any rate among representatives of the genus Tristoma, is not at all a simple formation but consists of a number of independent folliculi each opening by an independent duct into a special chamber located near the anterior edge of the entire complex (Fig. 314).

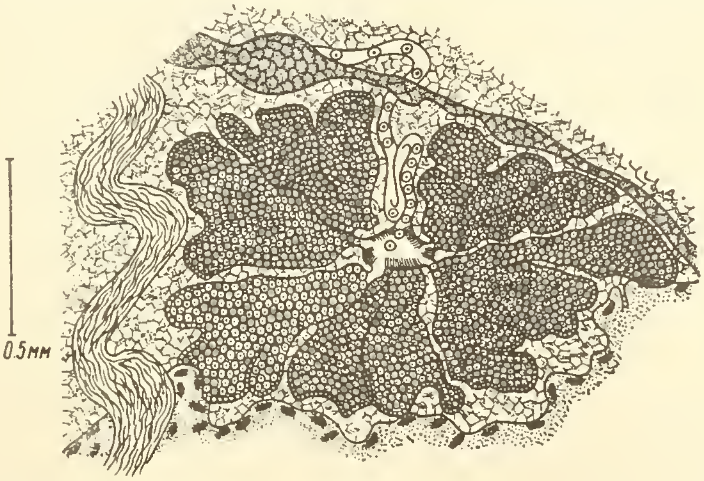

Fig. 314. Tristoma coccineum Cuvier, the ovary of the worm from the gills of Xiphias sp. from the region of the Island of Madeira (Atlantic Ocean).

The ovary, both in Loimoidae (see page 415) and Chimaericolidae (see page 415), has, according to the newest data, a follicular structure. Thus, among Monogenoidea this type of ovary is distributed in a number of groups very distant from each other. The structure of the ovary of such a type resembles very closely that which exists in Gyrocotylidae and Cestoidea s. str. In addition to that, the presence of a special chamber in Tristoma, about which we have just spoken, is very similar to the ovifunnel of tapeworms. In conclusion the sharpest difference between Monogenoidea and Cestoidea, about which we have written, is considerably reduced and cannot be considered as very meaningful. One should not attach great significance to the differences in the location of the sex apertures, for in monogenetic trematodes we can cite at the present time a number of examples of considerable variability of p. 476
the relations between the male sex opening and the openings of the uterus and the vagina. Thus, among many Capsalidae the rapproachement of all three sex apertures takes place. In Anthocotylidae the opening of the uterus lies on the side of the body and the male sex aperture on the ventral side along the medial line. Among certain highest Oligonchoinea there are also analogous relations and the atrium, which is common for all three apertures, is encountered in a number of the highest and lowest Monogenoidea. The

correlation between the male sex opening and the opening of the uterus in Dionchidae (see page 372) is completely analogous to the one existing in tapeworms.

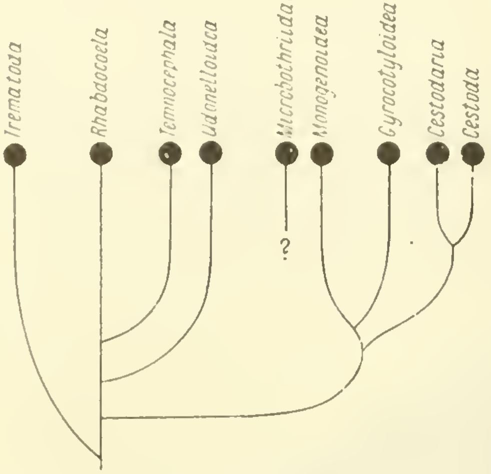

Fig. 315. Diagram of the correlations of the classes of flatworms. Microbothriidae are set apart to show the problematic status of their position.

We consider the difference in the structures of the copulatory organ as an important difference between Monogenoidea and Cestoidea; however, during the study of Diclybothriidae we found that actually the copulatory organ of these worms should be evaluated more as a cirrus than as a penis (Bychowsky and Gussew, 1950), consequently the sharp difference caused by this characteristic between Monogenoidea and Cestoidea s. str. is effaced.

Relatively recently an interesting study on Gyrocotylidae (Lynch, 1945) was published. The author studied the morphology of these interesting animals in detail and in the section on taxonomic position of genus Gyrocotyle indicates that they are undoubtedly close to monogenetic trematodes, but that they can be ascribed to tapeworms only provisionally. The author was not acquainted with our work which undoubtedly is interesting on the one hand because his conclusions are completely independent, but on the other hand this did not allow him to express a more definite judgment.

Thus, newer research apparently confirms the idea advanced by us about the great independence of Gyrocotylidae and their intermediary position between Monogenoidea and Cestoidea more and more. At the same time one cannot fail to note that their proximity to the first class perhaps is considerably larger than to the second.

In the analysis of the interrelations of parasitic flatworms, as is known, we have attributed enormous deciding significance to the cercomere and its chitinous armature. In 1952 A. V. Ivanov published a study on Udonellidae, which was conducted by him at our suggestion for the establishment of their position in the system of flatworms. As a result of very meticulous analysis A. V. Ivanov clarifies that this group descended from Turbellaria quite independently he separates it into a separate class. The basic criterion for such a conclusion apparently was precisely the absence in Udonellidae of a larva equipped with a cercomere and its chitinous armature. Agreeing with the point of view advanced by us, A. V. Ivanov, in the concluding part of his work, cites the diagram of phylogenetic relations between the main groups of flatworms. This scheme is principally very p. 477

close to one proposed by us in our work in 1937 and we fully agree with it. If one is to attempt to show on this diagram not only the correlations between the separate groups but also the degree of their divergency it will acquire the following aspects (Fig. 315) and will be understood without explanations.

The final question on which we would like to pause is the problem of the correlations of peculiarities of the biology of Monogenoidea and Cestoidea. We were told repeatedly about the circumstance that it is not understandable by what means this truly ectoparasitic group, which monogenetic trematodes represent, gives rise to such typical intestinal parasites as Gyrocotyloidea and tapeworms. It seems to us that it is possible to find sufficiently convincing, although to a certain extent conjectural answers to this question. Generally among monogenetic trematodes the transition to endoparasitism is far from being so rare as is usually pictured. Present representatives of the genus *Acolpenteron* are endoparasites parasitizing the ureters of their hosts. According to the studies of Ruszkowski (Ruszkowski, 1931), *Amphibdella torpedinis* Chatin has an obvious tendency towards the transition, be it partial, toward parasitizing the blood system of electric skates. The genus *Dictyocotyle* parasitizes the body cavity of skates (Nybelin, 1941). Numerous species of *Calicotyle* live near the cloacal opening of skates, appearing rather more as endoparasites than ectoparasites. A number of Polystomatidae parasitize the urinary bladder of Amphibia and Reptilia, etc. However, it is not these cases that present an interest from the point of view of the transition of ectoparasitism to parasitism in the intestinal cavity. This process it seems to us is connected with the transition of the very numerous monogenetic trematodes towards parasitizing from the gills to the surface of the buccal cavity of their hosts with subsequent advance to the walls of the pharynx and to the anterior part of the esophagus. Inasmuch as we can be sure that this process of transfer from ecto- to endoparasitism took place in the case which interests us among fishes and most probably in Selachii, one can suppose that the degree of differentiation of the separate parts of the intestines of the host could not serve as an important barrier for further advance of the worms from the esophagus to the intestinal tract. The fact that this is so is substantiated by the fact that among contemporary Selachii a number of species of tapeworms parasitize the entire length of the intestines--from the esophagus to its utmost posterior part without preference for any specific part. Thus, we have personally observed similar distribution along the intestinal tract in a number of Tetrarhynchidae.

As regards monogenetic trematodes, their tendency to transfer to parasitizing a cavity of the body and the anterior part of the intestines is encountered in Capsalidae, Monocotylidae, Polystomatidae, Hexostomatidae, and Dicliphoridae and others, i.e., among a very great number of morphologically varying forms which are related to both subclasses. As we have already written earlier, it is not possible to visualize the process of separation of the classes Gyrocotyloidea and Cestoidea directly from Monogenoidea. This would have been completely untrue, but the common ancestors of both apparently proceeded by way of adaptation to different peculiarities of parasitizing. The possibility of transfer from the initial ectoparasitism toward endoparasitism in the group of cercomeromorpha indicates to us certain peculiarities of the biology of the contemporary Monogenoidea.

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CONCLUSION

Let us draw certain conclusions. The problems of our research p. 47 were the working out of a system and the establishment of the basic trends of evolutionary process of monogenetic trematodes. The reconstruction of these ways in the absence of paleontological data is a very complex business, but unfortunately for the vast majority of groups of invertebrate animals one has to deal without them. The utilization of all available material which, through accumulation and superposition for comparisons and mutual correction, allows us to make more or less convincing conclusions is that much more important. It seemed to us that comparative anatomical data, data on the biology of adult animals, materials on postembryonic development, basic moments of the life cycle, occurrence of monogenetic trematodes on their hosts, indicating here also the information about the nature of fauna of Monogenoidea on determined large groupings of their hosts, and finally information about the phylogeny of their hosts, which is based on their paleontological remains, can serve as such material for the class under study for the purposes and aims that interest us.

During the analysis of the comparative anatomical data, we departed from two basic ideas which seem to us very fruitful for the attempts of the study of the phylogeny of any group. The first of them is the thought about the presence in each group of determined evolutionary tendencies, determined by morphological peculiarities of the group, which is developed in the changing conditions of the external medium in relation to the animal, and surrounding them. These evolutionary tendencies are reflected in the structure, not only of separate organs of their systems, but primarily of the entire organism as a whole. To show the presence of these tendencies within the limits of a particular group is a very rewarding problem and it seems to us that we succeeded in some measure in solving it in connection with the monogenetic trematodes.

The second idea which helped us in the comparative anatomical research of Monogenoidea from the point of view of the phylogenetecist is the theory of oligomerization of V. A. Dogiel. Its role is fully understandable. However, note that in our materials is indicated one more important principle about which we write in our review of the book of V. A. Dogiel (Bychowsky, 1955). This principle could be called the principle of the change of processes of oligomerization by the processes of polymerization. This principle, noted but not developed by V. A. Dogiel, allows us to understand a number of important peculiarities of the development of different groups of animals and also gives into the hands of the researcher materials for analysis of the reasons for the changes in the evolutionary direction of groups under examination. V. A. Dogiel was sympathetic to the consideration expressed by us on this subject and we hope that in the process of further p. 479 working out of the theory of oligomerization he will dedicate special study to these questions.

The data on the biology of Monogenoidea were utilized by us for the correction of the comparative anatomical materials and during the analysis of the occurrences of the worms on their hosts. Thus, this group of facts bore a purely auxiliary nature.

The business with materials on postembryonic development is quite different. As is known, the studies from the time of Mueller and especially Haekel represent the classical part of every phylogenetic research. In the analysis of these materials from the same position as in the relation of the comparative anatomical data it seems to us that we succeeded in obtaining very important general conclusions for the understanding of the phylogenesis of the groups. Inasmuch as the analysis of the postembryonic period proceeded in accordance with the comparative anatomical aspect it allowed us to establish with a great degree of probability the traits of the promonogenetic trematodes and the basic ways of divergence of the group. The latter was extremely important because it enabled us to conduct an analysis of the true homologies on the one hand and to establish the convergent similarities and parallelisms on the other.

It seems to us very important to apply the study of the life cycles of Monogenoidea during the establishment of the phylogenesis of the group. First of all we succeeded in showing that a complex life cycle is characteristic for Monogenoidea, not in the sense of the presence of a number of phases of development as in digenetic trematodes, tapeworms and other parasitic worms, but in the sense of its unusual adaptability to the life cycle of the host, chronologically as well as in relation to attachment to determined phases and stages of the life of the latter. These peculiarities of the life cycle indicate the duration of existence of the biological pair, parasite-host, which in its turn has a great phylogenetic significance. Thus, the analysis of life cycles yields important confirmations to those principles which are discovered during the analysis of the occurrence of the parasites on their hosts.

We have attributed great significance to the occurrence of Monogenoidea, and it seems to us that this was substantiated. The analysis of the nature of the distribution of monogenetic trematodes on their hosts showed their exclusive selective ability in relation to determined species and larger groups of hosts in natural conditions. Basing ourselves on these data we have analyzed the nature of the faunae of Monogenoidea on specific groups of hosts, and taking into consideration the data on the paleontological antiquity of the latter we established the time of appearance of the different groups of monogenetic trematodes on the corresponding groups of hosts. At the same time, what is especially important for the establishment of the phylogenesis of Monogenoidea, this analysis enabled us to answer the question about which groups of worms were primarily connected with a given group of hosts and which--secondarily.

In conclusion, justaposing one group of facts with the other, we obtained the possibility of establishing basic ways of the phylogenetic development of the Monogenoidea. We believe, although numerous errors are unavoidable, that,nevertheless,basically the constructed phylogenetic scheme corresponds to all contemporary facts. Any attempt to build it otherwise will inevitably lead to contradiction with one or the other of the groups of facts mentioned above. Whether or not we were able to show this convincingly is another matter,and we leave this to the readers to judge.

In the process of research,we had to touch upon a number of general questions along with those specific ones, Thus, during the discussion of the conclusions in the chapter about occurrence the question about p. 480 specificity is especially examined. We have attempted to show that specificity, although it is a more general phenomenon in relation to occurrence, nevertheless the latter is not determined only by specificity but also by a number of completely different biological factors. With such an approach many phenomena connected with the process of the origin and evolution of parasitism become understandable. Hence, a somewhat different evaluation of the known "triad" of factors of the formation of the biocoenotic pair, parasite-host, of E. N. Pavolosky; of the "triad" which as a whole is very important for philosophical evaluation of correlations between the fortuitous and the unavoidable in the process of evolution of parasitism. Further the research on occurrence led us to the necessity of reexamination of the contemporary evaluation of the so-called "law" of Fuhrmann and the reestablishment of its correctness, but only as a particular case of the relations between the occurrence of the parasitic worms with the phylogenetic links of the latter and the phylogenesis of the hosts. Certain considerations, which seem to us not without interest, are cited also in the chapter about phylogenetic parallelism, which in our opinion can be determined only as a particular case of evolutionary changes of the biocoenotic pair, parasite-host.

During the analysis of the phylogenetic scheme of Monogenoidea we were obliged to dwell on certain evolutionary questions and first of all on the general directions of the evolutionary progress (Severtsov, 1939). Certain cases of the evolutionary development of Monogenoidea cannot be included into the well-known directions by way of aromorphoses, ideoadaptions and coenogenesis, and regress as our data show. To these one must attribute the gradual, very sharp qualitative change of the organization of the parasite which accompanied a considerable increase in the life level and morphological level, but without rapid change of the conditions of its existence. In some measure these changes can be compared with telomorphosis according to I. I. Schmalghauser (1940 and 1946); however, this is a special type of evolution which demands special study.

The study of the processes of evolution of monogenetic trematodes forced us also to turn our attention to the phenomenon of convergent similarities and especially of parallelisms. In the light of these data and the theory of V. A. Dogiel, we came to the conclusions about the necessity for more careful attention to the questions of the oriented (directed, *nobis*) development which is clearly observed in nature and can be fully explained from positions of dialectical materialism (*sic*, ? *nobis*).

All the general questions touched upon in the present work cannot be solved through the materials of the study of one group of animals (alone, *nobis*). They demand wide research in a number of groups, and can be solved more or less successfully only in this manner. We hope that in the future we will be able to return, be it only to certain of the general questions which were touched upon in the present work.

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